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General Editor: G. R. de Beer, M.A., B Sc.

SOCIAL BEHAVIOUR IN INSECTS

METHUEN'S MONOGRAPHS ON BIOLOGICAL SUBJECTS

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SOCIAL BEHAVIOUR IN INSECTS

BY

A. D. IMMS, M.A., D.Sc., F.R.S.

AUTHOR OF "A GENERAL TEXTBOOK OF ENTOMOLOGY," ETC.

WITH 20 ILLUSTRATIONS

METHUEN & CO. LTD.
36 ESSEX STREET W.C.
LONDON

First Published in 1931

PRINTED IN GREAT BRITAIN

GENERAL PREFACE

BIOLOGY has long since reached the stage when it is impossible for one person to specialize in all its branches, or even to keep abreast of the latest developments in all of these. This is the more regrettable because it seems likely that many problems which baffle frontal attacks may be circumvented with the help of concepts and techniques of other branches of science, and that knowledge may thereby be extended. The present series of monographs attempts to give brief but authoritative accounts of the present states of knowledge in various departments of biology, and to convey information which can be obtained only at the cost of considerable time and trouble by a person who is not engaged in that particular branch. Teachers and students will find up-to-date accounts of their own subjects, and research workers will be aware of the progress made by their colleagues in other departments. At the same time, the general reader with a taste for biology will be able to follow the most recent developments in the various branches of the science.

G. R. DE B.

MERTON COLLEGE
February, 1931

PREFACE

THE habits and economy of social insects form one of the most remarkable chapters in biology. Their manifestations exemplify the heights to which mutualism and co-operation can attain, even when determined by causes other than intelligence. Since the social organization of insects has been evolved on a physiological and instinctive basis, it can be reviewed with greater detachment and impartiality than the more complex human system, which presents accomplishments that have been developed and integrated along a different line. The fact that the independent communal organizations of insects and man present many features in common, widens the horizon of our subject, and brings it into relations with both sociology and psychology. To the biologist social insects present no lack of fundamental problems with which he is directly concerned. Among them are displayed many functional adaptations, peculiar developments of symbiosis and the most complex and advanced phases of polymorphism. He is exercised with the problem as to how to account for the regular production of sterile individuals, generation after generation, and its relation to nutritional influences on the one hand and to hereditary factors on the other. Students of animal behaviour find in such creatures the culminating expression of instinctive habits. Practically-minded people preserve the hive bee for economic reasons : with the rest of such fauna they are exercised,

either with means of its extermination, or with leaving it severely alone.

This little book endeavours to present an outline of the essential features of the structure and habits of social insects: the main paths which their evolution has traversed and the basis upon which their behaviour depends. Effort has been made to avoid undue technicality and to present the subject in a form acceptable to readers other than entomological specialists.

It is difficult to imagine any present-day author of a book on social insects who can afford to neglect the works and expositions of Prof. W. M. Wheeler. Possessing a unique acquaintance with all that pertains to the lives of such animals, and philosophic insight in interpreting their behaviour, Prof. Wheeler has done much to co-ordinate, and bring into daylight, a subject of perennial interest. Opportunity, therefore, is taken here to express, to my distinguished friend at Harvard University, indebtedness to his influence, without which this book would not have been written.

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A. D. IMMS

HARPENDEN, HERTS
January, 1931

CONTENTS

SOCIAL BEHAVIOUR IN INSECTS

CHAPTER I

THE SENSE ORGANS AND INSECT BEHAVIOUR

THE behaviour of an insect, as of any other animal, consists of acts which are the ultimate effects of stimuli upon its particular type of anatomical structure. The stimuli themselves originate either from the environmental forces of the outer world or from causes operating within the insect's body. External stimuli act very largely through the organs of sense, which are special receptors for the purpose, whereas internal stimuli arise from biochemical activities going on within the tissues.

The most usual reactions to external forces are by movements. A given stimulus impresses itself upon the sensory cells concerned, and an impulse is conveyed by afferent nerve fibres to an association centre located within the central nervous system. The association centre, in its turn, is linked up with a motor centre which sends out afferent nerve fibres terminating in a muscle or group of muscles (Fig. 1). The association centre is a kind of two-way connexion between the roots of the sensory and motor nerves. Its degree of development varies greatly, and in the brain, for example, there is a large number of such centres whose nerve

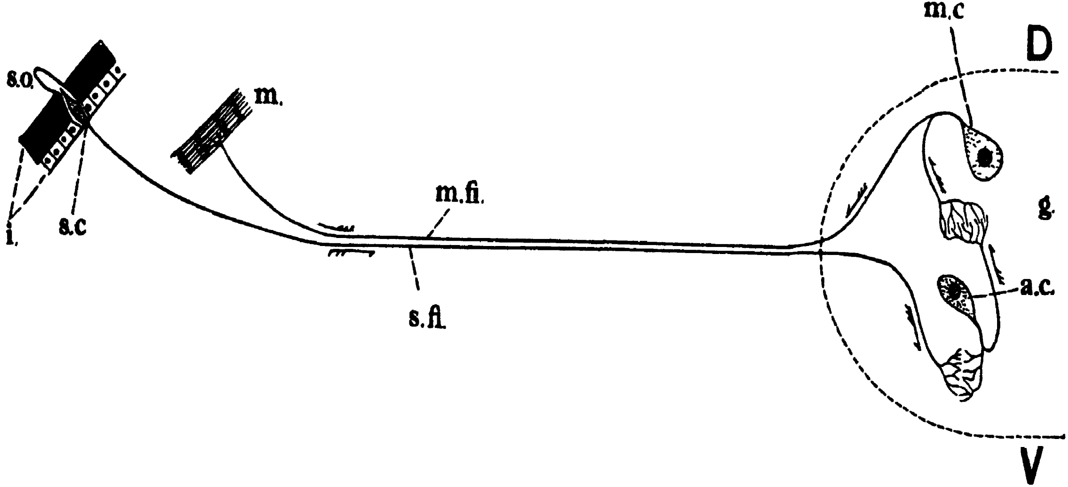


Fig. 1.—Diagram of the Reflex Mechanism of the Nervous System of an Insect

One half of a ganglion, *g.* of the ventral nerve cord is represented in outline. *D*, dorsal aspect; *V*, ventral aspect. A motor fibre (*m.fi.*) and a sensory fibre (*s.fi.*) of a lateral nerve are shown; *i.*, integument; *s.o.*, sense organ; *s.c.*, sensory cyton or cell; *m.*, muscle; *a.c.*, association cyton; *m.c.*, motor cyton. (The course traversed by a stimulus, received by the sense organ, is represented by arrows.)

fibres link different parts of the nervous system together. This type of nervous mechanism, known as the composite reflex arc, prevails in all animals with a central nervous system, differing only in its degree of elaboration. In insects, however, there is this difference as compared with vertebrates. The only known afferent nerve-cells are peripheral in situation and none have been found in the central ganglia as in vertebrates : their fibres when traced to their particular ganglionic centre end in terminal arborizations. Whether this distinction is a fundamental one we are not in a position to say, since histologists have paid too little attention to the origin and growth of the finer components of the insect nervous system.

By no means all stimuli affecting insects originate from the outside. Whether their bodies contain anything comparable with the endocrine glands of vertebrates, that control important phases of growth and behaviour, is unknown. There are, however, certain ductless organs, which appear to be glandular in function, that are almost universally present among insects. The corpora allata, or small paired bodies, present in close relation with the sympathetic nervous system, and the œnocytes, which are segmentally grouped nests of highly specialized cells, may possibly be important in this respect. All that is known is that internal stimuli exercise a profound influence upon insect behaviour, but as regards the nature and sources of these stimuli we are completely ignorant. Such stimuli are most probably products of metabolism which function as messengers activating or modifying specific phases of behaviour. Many instincts are initiated in this way as, for example, those involved in the processes of cocoon-formation and of oviposition, and in the transformation of the caterpillar into the chrysalis : internal stimuli further deter-

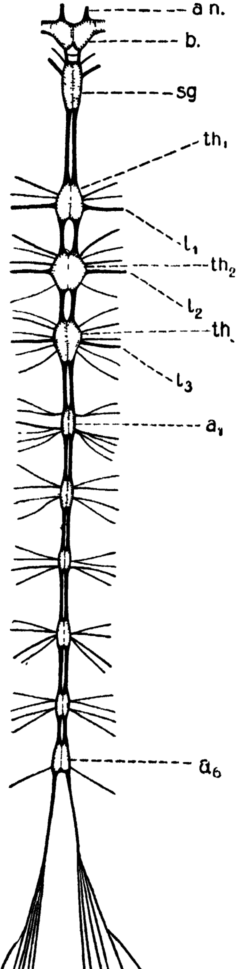


FIG. 2.—Central Nervous System of an Earwig

a.n., antennary nerve; *b.*, brain; *sg.*, subœsophageal ganglion: th_1–th_3, thoracic and a_1, a_6 abdominal ganglia, forming the ventral nerve cord; l_1–l_3, nerves to the three pairs of legs.

mine differences in reactions to the same external forces during different phases of an insect's life, and other features of behaviour.

The Nervous System

The central nervous system of an insect (Fig. 2) consists of a dorsal ganglionic centre, the cerebral ganglion or brain, which is situated in the head immediately above the œsophagus. The brain is joined by means of a pair of lateral nerve connectives with a ventral or subœsophageal ganglion, located beneath the œsophagus. The latter ganglion is united by paired longitudinal connectives with a chain of ganglia forming collectively the ventral nerve cord. For the most part there is a separate pair of ganglia to each segment of the body but, in different insects, a varying amount of fusion between adjacent ganglia takes place, particularly between those at the posterior extremity of the ventral chain. A visceral or sympathetic nervous system is also present, together with a peripheral sensory system innervating the integument.

The brain (Fig. 3) is the principal seat of sensation and is also the most important co-ordinating centre of the body. All investigators have observed the large number of sensory and motor nerve tracts, from different regions of the body, that enter and become localized in the brain. These are concentrated in a pair of special areas termed the mushroom bodies, and there is good reason for believing that, in these bodies, the main sensory impressions are recorded, actions are co-ordinated and associations once acquired are impressed. The greatest development of the mushroom bodies is found in the order Hymenoptera: here they attain a size and complexity not found elsewhere, and it is in this order that psychic development attains its highest

expression. In the Hymenoptera, and in some other orders, the size and complexity of the mushroom bodies corresponds in a general way with complexity and specialization of behaviour or, in other words, they

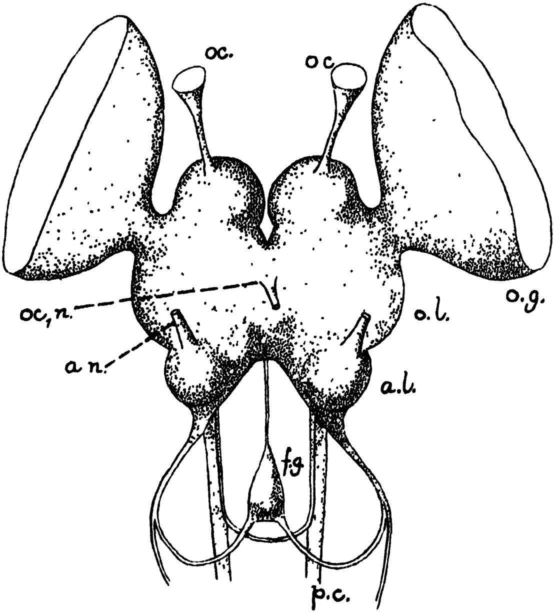


FIG. 3.—Frontal View of the Brain of a Locust

a.l., antennary or olfactory lobe ; *a.n.*, antennary nerve ; *f.g.*, frontal ganglion of sympathetic system ; *oc.*, lateral ocelli and nerves ; *oc, n.*, nerve to median ocellus ; *o.l.*, optic lobe ; *o.g.*, optic ganglion ; *p.c.*, connective to subœsophageal ganglion. From Burgess.

provide a kind of mental index: One of the most experienced insect neurologists, Jonescu, has shown that the mushroom bodies are more greatly developed in the worker hive bee than in either the drone or the queen—a fact that would be expected if they are the centres of

instinctive behaviour. Other investigators, notably von Alten, in 1910, and Armbruster, in 1919, have made comparative studies and careful measurements of the brain in various Hymenoptera. By taking numerically expressed relationships between two dimensions of the mushroom bodies, and a constant in the same brain, a kind of 'intelligence index' was obtained. If the Hymenoptera be arranged in an ascending series upon this basis, the sawflies come lowest on the list, the social Hymenoptera highest, while the solitary bees occupy an intermediate position. This conforms well to what is known of behaviour in those several groups.

The subœsophageal ganglion controls and co-ordinates the movements of the mouth-parts. The experiments of Kopéc suggest that it also functions as a reflex-inhibiting centre. After the excision of this ganglion very strong reflex movements result from certain artificial stimuli, whereas similar stimuli are ineffective in the uninjured insect. By decapitation, both the initiatory and inhibiting centres are lost, and headless insects can be artificially induced to perform complicated reflex acts.

Each ganglion of the ventral nerve cord is a reflex centre, combining both sensory and motor functions, with respect to its particular segment. In addition to its ganglionic autonomy, the ventral cord as a whole exhibits considerable powers of co-ordination. It is this capacity which enables a decapitated insect to walk, fly, lay its eggs, and perform other actions, provided requisite artificial stimulation be applied. Their normal initiation and full co-ordination, however, are not possible unless the brain be intact.

Sensory Perception

Insects are able to perceive very much the same stimuli which impart definite sensations in man. Such

stimuli make certain impressions upon the insects' nervous system which result in their behaving accordingly. Light, chemical stimuli (smell, taste), tactile stimuli and sound vibrations exercise their respective influences to a varying extent among different species. There are no grounds, however, for concluding that these impressions bear any real resemblance to those which we ourselves perceive. One of the most important differences lies in their reactions to different amplitudes of these stimuli which involve ranges outside human capacity. Insects respond, for example, to chemical stimuli too dilute or too delicate for perception by our olfactory or gustatory organs : they react in some cases to pitches of sound incapable of appreciation by the human auditory organ : and their range of colour discrimination does not involve the whole spectrum visible to human beings, yet, at the same time, they are able to appreciate ultra-violet rays. Whether sensory reaction in insects also embraces responses to other types of stimuli, imperceptible to human senses, is a possibility which has often asserted itself without being, as yet, definitely proved.

The essential components of a sense organ are known as sensillæ. The most generalized types of sense organs consist of single sensillæ only, while in their more complex developments large numbers of these elements become compacted together to form highly evolved localized structures. A sensilla always exists in relation with the external cuticle and consists of a specialized hypodermal (epidermal) cell, connected with the fibre of a sensory nerve. In association there are usually one or more unmodified hypodermal cells, and the whole is invested externally by a differentiated portion of the cuticular covering of the body (Fig. 4). The simplest and most primitive sensillæ are merely innervated hairs, and a

number of different kinds are believed to be modified derivatives from this type. Since their functions are often problematical, they derive their names from the prevailing form assumed by their cuticular parts (Fig. 5). Thus, we have not only trichoid or hair-like sensillæ, but also placoid, basiconic, cœloconic, ampullaceous, campaniform and other forms of sensillæ.

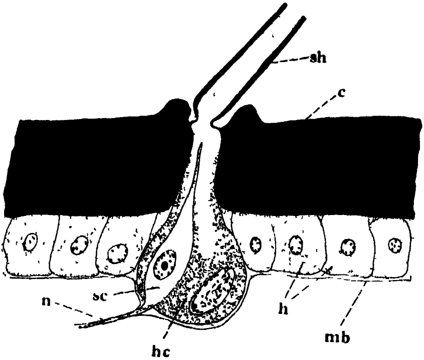


FIG. 4.—Schematic Section through the Integument of an Insect including an Innervated Hair which forms the simplest type of Sensilla

c, cuticle; *h*, hypodermis; *hc*, hair-forming cell; *mb*, basement membrane; *n*, nerve fibre; *sc*, sense cell; *sh*, base of sensory hair.

The organs for light perception comprise the compound eyes and the ocelli. The compound eyes are innervated from the optic lobes of the brain and are composed of variable numbers of individual visual sensillæ termed ommatidia. In aberrant or degenerate insects only a few ommatidia, or even a single one, may compose the eye, but usually these elements are much more numerous and may range up to 20,000, or even more. Notwithstanding its prevailing complexity of structure, the

compound eye is a less perfect optical instrument than the vertebrate eye, for the reason that it is devoid of a focussing mechanism. Its capacity for image formation is only effective within a very limited focal range, while the distinctness of the image depends partly upon the

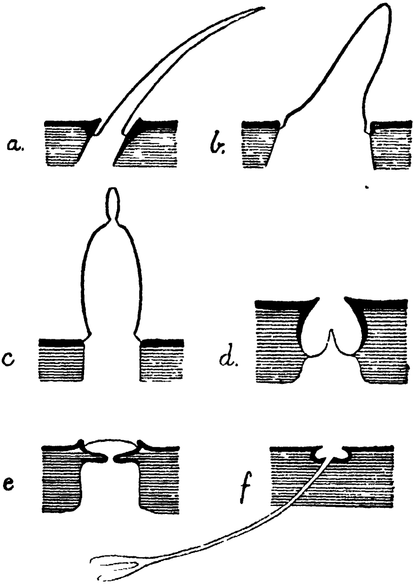


FIG. 5.—Cuticular Portions of Sensillæ of Various Types

a., trichoid ; *b.*, basiconic ; *c.*, styloconic ; *d.*, cœloconic ; *e.*, placoid ; *f.*, ampullaceous. From Imms.

nearness of the object viewed and the number of ommatidia involved. An eye composed of a large number of small ommatidia will, on the mosaic theory, produce a sharper and more detailed image than one of similar size, but formed of less numerous, larger

ommatidia. There is evidence that general perception, particularly of movement, is more important in the lives of insects than a capacity for image formation. Many insects possess, in addition, ocelli, and the only type of these organs which need concern us here are the dorsal ocelli, located between the compound eyes. They are innervated from the brain independently of the compound eyes, and appear to be adapted for vision in darkness or greatly diminished light, as well as having some power of perceiving very near objects. It is possible that they supplement the function of the compound eyes in species bearing ocelli, the unaided compound eyes being unable to fulfil the whole range of visual requirements.

Chemical stimuli affect the organs of smell and taste: smell is perception at a distance, while with taste actual and more intimate contact with the stimulus is involved. The words 'smell' and 'taste' savour too much of anthropomorphism to be strictly applicable in the case of insects, whose olfactory and gustatory senses seem largely to intergrade. Chemical receptor organs consist for the most part of isolated sensillæ—they are far less often grouped to form more elaborate structures. Various types of sensillæ—placoid, campaniform, cœloconic, etc.—have been credited with odour perception. Large numbers are located on the antennæ and, for this reason, the latter appendages are very commonly regarded as being olfactory in function. Others, situated on the mouth-parts, have been credited with a gustatory function. Forel has stressed the fact that the presence of large numbers of such organs, externally on the antennæ which freely project from the body, appears to impart to the insect wider powers of perception of chemical stimuli than if the latter had to penetrate within the recesses of an olfactory chamber, as in ter-

restrial vertebrates. It is true that responses to chemical stimuli (odours) play a preponderating rôle in the lives of most insects. They are specially in evidence in the selection of food, in the choice of suitable media for egg-laying ; in the discovery of the female by the male, often at a considerable distance ; and in recognition among individual members of a society or colony. During recent years McIndoo, in the United States, has contested the view that the antennæ in general are the seat of odour perception. He claims that the sensillæ involved are of a type which is more generally present on the legs and the bases of the wings, and other regions of the body. While his researches indicate that response, in some form or other, to chemical stimuli is by no means confined to the antennæ, they are not sufficiently convincing to discount the accumulated evidence of other investigators that these appendages are principally concerned in the process.

While there is good reason for concluding that chemical stimuli may be appreciated by the antennæ (and also by the palpi) both at a distance, and by actual contact, this type of perception seems to be very different from either the olfactory or gustatory senses of man. So far as we know, sensillæ located on these insect appendages have their surfaces dry, and consequently solution of the chemical stimulant in an external bathing fluid is not involved. It is possible, however, that a gustatory sense more nearly akin to that of man is also present, since groups of sensillæ occur on the lining membrane of the oral and pharyngeal cavities, which can scarcely be credited with any other function. A capacity for detecting even minute differences in the percentage constitution of non-odorous liquids, by actual contact, is known to occur in *Vanessa* butterflies and other insects from the researches of Minnich. In the butterflies, the

tarsi exhibit keen perception of this kind, and here we have a type of sensory reaction unknown outside the arthropods.

The tactile sense in insects is largely located in the antennæ, and the sensillæ involved are very commonly of the nature of fine sensory hairs. They also occur distributed over other regions of the body and its appendages. A moving insect, with well-developed antennæ, has these appendages in constant agitation while exploring each fresh surface or object in its path. Tactile sensillæ, however, are commonly intimately mingled with others that are attuned to perceive chemical stimuli. It frequently happens that an insect comes into contact with substances which affect both kinds of sensillæ. The resulting impressions are, as it were, composite and become conveyed by the afferent fibres of the antennary nerve to association centres in the brain. Here it is probable that they are combined in a single contact-odour sense which, according to Forel, plays so important a rôle in the social behaviour of ants.

Insects pertaining to diverse groups are known to respond to aerial vibrations, and some possess a capacity for sound-production themselves. Creatures such as grasshoppers and their allies, and cicadas, are provided with elaborate sound-receptors known as tympanal organs. The sensory structures associated with these organs are known as chordotonal sensillæ. Each sensilla is a kind of ligament usually fixed at its extremities within the body: it contains a special sense cell in connexion with a sense-rod or scolopale. The scolopale is believed to be free to vibrate in response to suitable stimuli, since it is surrounded by fluid. Other insects, such as ants, possess far less elaborate organs, while either grouped or isolated sensillæ are frequent in different regions of the body in many insects. Eggers,

who is the most experienced investigator of these organs, concludes that, in their simplest condition, they function as 'rhythmometers' co-ordinating and regulating rhythmic muscular activities in the body. Whether this be the case or not, the general similarity of structure of these sensillæ whether isolated, or combined in relation with highly evolved tympana, suggests a similarity of basic function. It would, therefore, appear probable that, in all cases, they respond, in some way or other, to vibratory stimuli in varying degrees.

It needs to be realized that an exact knowledge of the functions of insect sensillæ is as yet but meagre, notwithstanding the bulk of the literature that exists on the subject. The minute size of these organs, together with their scattered and often intermingled distribution, present immense difficulties in the way of controlled experiments designed to explore the repertory of sensory perception in the living creatures.

The Fundamentals of Behaviour

Up to this point mechanism has been the prime consideration, and we may now deal briefly with what happens when this machinery is put into full action. By this is meant behaviour. It will be convenient to group this subject into the three main phases under which it manifests itself in insects, emphasizing at the same time that these phases are not clear cut but grade one into the other.

1. **Reflex Behaviour**—It is well known that the most elementary kinds of animal behaviour are reflexes which are innate, involuntary actions depending upon the nervous mechanism. Reflexes usually involve responses by organs or parts rather than from the animal as a whole, and are not specially concerned with its orientation in relation to any given stimulus. Many

authorities distinguish between reflexes and tropisms—a subject which has been much contested. The word tropism means a turning: it is an automatic act but differs from an ordinary reflex in that the animal, as a whole, responds to a given stimulus by orienting or turning itself in a definite direction with respect to that stimulus. Tropisms are particularly evident in the behaviour of the Protozoa and lower invertebrata. Their characteristics have been well explored by Loeb, and it may be said that clearly defined examples become less frequent as we ascend the animal scale. In many cases they are modified, or almost deleted, by combinations of reflexes so as to be no longer recognizable. Clear examples of insect tropisms are seen in the automatic or forced movements of a moth towards an artificial light, and in the directional reactions of blow-fly larvæ towards specific food odours.

2. **Instinctive Behaviour**—Instinctive acts involve the organism as a whole and are formed as a chain or series of co-ordinated reflexes. A number of different reflexes may be involved in an apparently simple act, and it becomes by no means obvious whether such an act consists merely of these elementary phases or is, in fact, the expression of a definite instinct. Instinctive behaviour, however, is correlated with the presence of a brain. If the brain of an insect be removed the actions of the creature when stimulated consist solely of reflexes. A brainless insect will eat if food be placed in contact with its mouth organs, but it has no power of seeking food when the latter is placed even a very short distance away. A decapitated insect, when in the right physiological condition, can be induced to exhibit a series of reflexes indistinguishable from normal oviposition—provided it be suitably stimulated artificially. The full egg-laying instinct, however, is not invoked unless the

nervous system be intact. The brain, in other words. receives the primary stimuli, internal or external, which enables it to give the initiative impulse, or activating force, which sets going a given chain of reflexes. The whole combined set of actions constitutes the expression of an instinct. What actually directs and co-ordinates grouped reflexes, so that they become instinctive acts, will not be discussed here. It may satisfy some of us to term it merely ' impulse ', but others may join with Driesch in calling it entelechy or its equivalent.

3. **Plastic Behaviour**—Whereas reflex and instinctive behaviour are ordinarily automatic, and inborn, there are actions betrayed by insects that are modifiable, or plastic, in that they vary adaptively in response to environmental requirements. It is in the higher manifestations of plastic behaviour among insects that we see actions betrayed which are commonly attributed to ' intelligence '. Plastic behaviour attains its highest expression among these animals in the social species. It would appear that more perfect inhibitory and controlling means have been evolved in their central nervous system so that they have become released from some of the rigid responses of the purely reflex kind, and are thereby enabled to display more modifiable actions.

Plastic behaviour evinces itself in many ways and the subject has been treated at length by numerous observers, including Forel, Wheeler, Ferton, the Peckhams, and Bouvier, to mention but a few. Experiences accumulated during the life, both of the species and of the individual, play a definite part. They depend upon what may be termed ' organic memory ' and its associations. In its racial phase organic memory comes into play in rhythmic behaviour, which betrays itself by all the individuals of a species acting alike at definite time intervals, irrespective of whether the original stimulus

be present or not. Many moths, for example, will remain quiet and motionless in a dark room throughout the day and, without any change in illumination, will become active at a regular time each night. Individual organic memory is another phase of the same behaviour. A cockroach, for example, seeks dark places, but it can be driven away by administering a slight electric shock, each time it attempts to enter such a place from a lightened chamber. The insect soon learns to associate the shock with dark places and restrains its habit of resorting to them. It has further been shown that this is a true example of plastic behaviour and not a case of the reversal of a tropism induced by electricity. Von Frisch was able to train the hive bee so that it associated a certain colour with the position of its food. The natural foraging and homing habits of ants unquestionably involve an associated memory of topography, and many other examples of organic memory have been recorded.

The higher examples of plastic behaviour involve the spontaneous alteration of instincts in relation to special circumstances. It will suffice to quote an observation by J. H. Fabre respecting the sacred Scarab. This beetle normally frequents stony plateaux, where it constructs a pyriform mass of sheep dung to contain its egg. When completed the mass is rolled to a spot that can be excavated and where it can be buried and watched over. Some examples of the Scarab were transferred by Fabre to cages containing soft soil, and under these conditions they constructed the excavations first, then gathered the dung and moulded this material within the chambers into the necessary pyriform masses. It is in spontaneous adaptive acts of this kind that the higher types of insect behaviour betray themselves and many similar examples have been recorded.

This preamble on behaviour will pave the way to the main subject of the evolution of social habits. Some warning may be opportune here because we have to avoid the pitfalls of the pure experimentalist who studies social insects as isolated individuals : and of the observer who only notes their behaviour in their natural communistic life. The one is liable to interpret behaviour too exclusively on the basis of reflexes, while the other may be prone to credit higher psychological implications than may be actually warranted.

CHAPTER II

THE BEGINNINGS OF SOCIAL INSTINCTS

APPROXIMATELY half a million species of insects have, so far, been discovered and named. The habits of the vast majority of this assemblage are essentially of the solitary kind. Except for purposes of coition, the sexes have no association with each other. The female parent, having deposited her eggs, has no further concern for their future or any contact with her offspring. Once her eggs are laid her life soon terminates, while the individuals of the resulting progeny work out their own salvation, each leading an independent existence. On the other hand, there is a relatively small proportion of species, about 6,000 in round numbers, that are definitely social in their habits. Between these two extremes various species are found whose habits betray graded series or tendencies towards an incipiently social existence—they are, in fact, subsocial rather than truly social. These latter are of particular significance because we are able to trace in them the beginnings of social behaviour.

Before proceeding further it is necessary to define what is implied by the expression social insect. It is an insect which lives in society: each society consists of the two parents, or at least the fecundated female, and their offspring, and the two generations live to a varying extent in mutual co-operation in a common abode or shelter. In social insects it consequently fol-

lows that there is a lengthening of the adult or parental life so as to allow of this definitive association with the progeny.

The merely gregarious habit, which prevails in some insects, has nothing to do with the evolution of social behaviour. Certain species of caterpillars live gregariously and even act in mutual co-operation : lady-birds mass together prior to hibernation, while locusts become gregarious when they assume their migratory swarming phase. These are temporary habits which prevail without involving any association of parents and offspring.

Subsocial habits are betrayed among species belonging to a number of different groups of insects : each group, in fact, represents a separate and independent attempt to forsake the purely solitary mode of life. In the majority of cases not very much beyond rudimentary beginnings of social organization has taken place but, nevertheless, these beginnings foreshadow some of the essential features that characterize the highest expression of social behaviour. In order to appreciate the full significance of our subject, it is necessary first to consider a few examples among these subsocial forms before proceeding to the main theme. The common European earwig (*Forficula auricularia*), for instance, deposits her eggs in a mass in an excavation, she has previously prepared, below the surface of the soil. She rests over them until they hatch and the young remain for a few days with the parent, who in this respect resembles a hen with her brood of chickens, and her association with her progeny is maintained until they disperse. The present writer has recorded very similar behaviour among the Embioptera, which are a very restricted order of tropical or subtropical insects comprising the so-called web-spinners. The Himalayan species, *Embia major*, inhabits

dense silken tunnels which it constructs beneath stones. The female lives in close association with the eggs and young, protecting them as far as possible by means of her body. If alarmed and driven away she returns sooner or later to take up the same attitude. When the young reach the second stage of growth, they exhibit a tendency to wander from the immediate vicinity of the female and construct adjacent tunnels for themselves. The whole colony is social in tendency, and as many as twenty-one adult individuals have been found inhabiting a compound nest of interlacing passages. The females, moreover, are wingless and seem to be rarely discovered outside these habitations.

Among beetles, in the Scarabæid, *Copris lunaris*, the male and female associate in pairs: they excavate an earthen chamber which they fill with ellipsoidal balls of dung and in each of which an egg is deposited. These are guarded while the larvæ are devouring the food thus provided, and, when the young beetles emerge, they are escorted to the exterior by the parents, and the original family then becomes dispersed. There are other species of *Copris*, and allied dung beetles, such as *Geotrupes*, *Minotaurus* and *Onthophagus*, which exhibit very similar parental behaviour, more or less highly developed in the several cases.

One of the more recently discovered examples of sub-social habits is afforded by certain beetles of the family Cucujidæ. These were found by Wheeler to live, along with their brood, in the hollow leaf-stalks of young *Tachigalia* trees in British Guiana. The parent beetles feed along strands of specially nutritive tissue which they eat out into grooves. Sooner or later the colony becomes increased by numbers of mealy-bugs (*Pseudococcus*) which wander into the leaf-stalk through the original opening gnawed by the beetles. They settle

down in the groove-like channels eaten out by the beetles, and feed on the nutritive tissue. The beetles lay their eggs and their larvæ devour similar food to that of the parents. The instinctive behaviour of both the larvæ and their parents is specially noteworthy, since their habits are sufficiently plastic to learn to stroke the mealy-bugs with their antennæ, thus stimulating them to discharge honey-dew which they eagerly consume. The beetle larvæ turn into pupæ in due course in the petioles, and when the young beetles emerge they remain with their parents, but soon commence egg-laying on their own account. The result is that there is eventually a community of beetles, larvæ, pupæ and mealy-bugs of diverse ages living together. When the original habitation becomes overcrowded, pairs of young beetles forsake it and discover other *Tachigalia* leaf-stalks wherein they found new colonies.

A final instance of subsocial behaviour, and of a somewhat more highly evolved character, may be mentioned. In this example we are concerned with solitary wasps of the genus *Scleroderma* (family Bethylidæ) whose habits have been investigated by Bridwell in Hawaii and by Wheeler in the United States. The species *S. macrogaster*, observed by Wheeler, was reared on beetle larvæ, particularly those of the hickory borer (*Cyllene pictus*). The female *Scleroderma* when offered a *Cyllene* larva bites and stings it, over different regions of its body, until it is paralysed. She feeds for several days on its blood, which exudes in minute droplets from the already made sting punctures. Soon afterwards she begins to lay a number of eggs on the living, but motionless, body of the prey, and, upon hatching, the larva insert their heads through the integument of the prey or host and imbibe its blood. The parent *Scleroderma* remains with the brood, often standing over them and

sometimes licking them. Occasionally she resorts to drinking the host's blood which exudes around the spots where her progeny are feeding. When the larvæ are mature they spin cocoons and pupate around the now defunct host, and the wasps which emerge repeat the foregoing behaviour on their own account. The original parent is long-lived and capable of bringing up several broods. Wheeler states that when she and her female offspring, or several females of different parentage, are confined in the same vial with a *Cyllene* larva, there is no rivalry ; on the other hand, they co-operate among themselves in paralysing the prey which serves as the common source of food for their collective offspring.

Sporadic manifestations of the kind exemplified are clearly not chance associations of individuals of the same species. They are, in fact, developments on a family basis which is the true foundation of the beginnings of social behaviour. We have seen that the life of the female parent and, in some cases, of the male also, becomes sufficiently prolonged to allow of actual relations with the offspring. The latter, along with the parent insects, are lodged in a common abode or nest and may share common food. There are, however, as yet no indications of real co-operation between parent and offspring for the mutual benefit of the colony. Also, as we shall see later, there is no indication of any specialization of function, with concomitant differences of structure, among individuals of these incipient families, which play so predominating a feature in social organization.

The causes that contribute to the lengthening of the life-span of the female parent are obscure. Perhaps, as Pearl and Wheeler believe, decreased metabolic activity may be partially accountable. An environment beneath the soil, in cavities in wood, or in manufactured nests is characterized by darkness, reduction of oxygen supply,

a uniform and on the whole rather low temperature, and a tolerably constant humidity. Muscular movement under such conditions tends to become less active and katabolism is lowered in consequence. Anabolic functions may tend to become enhanced as is shown in the accumulation of fat-body. It would seem that the more pronounced these environmental conditions become, the longer is the parental life, which, in the case of ants and termites, may be prolonged for a number of years.

The mutual association of different individuals of a species tends to promote fresh reflexes and, in turn, additional instinctive acts which are not engendered in the lives of solitary species. Even gregarious caterpillars betray signs of co-ordinated behaviour among themselves and in the massing of ladybirds contact reflexes are invoked which play no part in their earlier life. With subsocial insects such reflexes and instincts have already assumed a higher plane, and it cannot be overlooked that the development of the social organization has only been possible as the result of the same causes. The failure of subsocial species to travel very far along the track of organized communal life, in so many cases, seems to be due to a considerable degree to absence of the inherent capacity for evolving the higher nervous mechanism required. Social life attains its highest and most diversified expression among the Hymenoptera which, as we have already seen, exhibit cerebral development in its most complex condition.

The various groups which comprise subsocial or social species represent seven different natural orders of insects. In the following scheme these groups are individually enumerated and their positions in the general system of insect classification will become apparent. Orders comprising true social forms are indicated in heavier type.

Division I. *EXOPTERYGOTA*

(*Insects undergoing incomplete metamorphosis and whose wings develop externally to the body.*)

Order ORTHOPTERA. Subsocial species occur in the family Blattidæ or cockroaches and in mole crickets (*Gryllotalpa*) in the family Gryllidæ.

Order DERMAPTERA. Subsocial species among earwigs of the family Forficulidæ.

Order **Isoptera.** Comprises the termites whose species are divisible into three families, all of which are social.

Order EMBIOPTERA. Comprises the web-spinners : probably most, if not all, the species are subsocial.

Order PSOCOPTERA. In the tropical suborder Zoraptera, which is allied to the Psocidæ or book-lice, the species are subsocial, living in small colonies beneath bark, in decaying wood, humus, etc.

Division II. *ENDOPTERYGOTA*

(*Insects undergoing complete metamorphosis and whose wings develop within the body, only becoming external at the pupal stage.*)

Order COLEOPTERA. Subsocial beetles are represented in the families Scarabæidæ, Passalidæ and Scolytidæ (including the Platypodidæ) and more rarely in the Cucujidæ and Tenebrionidæ.

Order **Hymenoptera.** The following families of solitary wasps betray subsocial habits : Bethylidæ, Sphecidæ, Trypoxylonidæ and Bembecidæ. In the Vespidæ are included all the true social wasps.

Among bees the Andrenidæ are essentially solitary forms, but include social species in the subfamily Halictinæ. In the families Bombidæ and Apidæ all the species are truly social.

Among ants (Formicoidea) all the species are social.

It will be gathered, therefore, from the foregoing scheme that true social life has become developed in two orders only, viz., the Isoptera, or termites, and the Hymenoptera which include ants, bees and wasps. These orders are so divergently apart as regards every feature of their structure and metamorphosis, that they lie almost at the two poles in all schemes of insect classification. In the case of the Isoptera we have a lowly archaic group whose affinities lie nearer to the Blattidæ or cockroaches than to any other insects : the Hymenoptera, on the other hand, rank among the most specialized and highly developed of the whole class. It is remarkable, as will be seen in the pages to follow, that the evolutionary plan, moulding the social life in these two such distantly related orders, has pursued paths that run so nearly parallel. As Wheeler aptly remarks, it is as if we had found, when Australia was discovered, the kangaroos and opossums enjoying a social organization like that of man.

In the next four chapters the four great divisions of the social insects, viz., wasps, bees, ants and termites, are separately dealt with. The wasps are selected for prior treatment because it is among them that the evolution of social behaviour in the Hymenoptera, as a whole, can be most advantageously followed. The termites are left until last for the reason that the phases of social organization displayed among them can be best appreciated in relation to those prevailing in the Hymenoptera.

CHAPTER III

WASPS AND THE EVOLUTION OF SOCIAL ORGANIZATION

IT has already been pointed out that, excepting the Isoptera or termites, true social insects belong to the order Hymenoptera. We may go further, in fact, and say that they are confined to a single division of that order viz., the Aculeata. This division includes the social and solitary wasps, the social and solitary bees and the ants. It is not easy, however, to draw a hard distinction between the Aculeata and the Terebrantia or parasitic Hymenoptera, from which they have been derived. The best distinguishing character lies in the ovipositor which, in almost all Aculeata, is modified to form a sting and is no longer used as an instrument for oviposition.

Altogether about 10,000 species of wasps are known. The structure and behaviour of the more primitive families indicate that it is among them that we have to look for the ancestors of both the bees and the ants. The study of wasps, therefore, is fundamental in understanding the evolution of the social Hymenoptera as a whole. Reference has already been made to the habits of subsocial wasps of the genus *Scleroderma*, belonging to the primitive family Bethylidæ. These wasps display the essential phases of social behaviour in a very rudimentary condition. The female parent is long-lived, associates with and even licks her progeny, and

is capable of rearing several successive broods. The offspring, moreover, shows some slight co-operation with the parent.

The true social wasps only number about 800 species and are all included in the single family Vespidæ. It is divided into nine subfamilies of which four are solitary or, at most, subsocial in habit, while the remaining five families exhibit different grades of social behaviour. The family as a whole is essentially carnivorous in habit, and its members utilize other insects as food for the brood. Having captured the prey the ovipositor is used as a sting and, by this means, poison is introduced into the victim, which operation has the effect of rendering it immobile, without necessarily killing it. Many of the higher wasps chew or malaxate the prey and, thus prepared, it is fed to the larvæ in dismembered portions. The carnivorous habit, however, is not quite universal and in the subfamily Masarinæ, whose species are solitary, the adults are anthophilous and feed the brood upon a honey and pollen mixture : in these habits they foreshadow the behaviour of bees.

Of the social subfamilies, the Stenogastrinæ are of particular interest. They are an Oriental and Australian group which has only been very partially investigated. It is evident, however, that they are transitional between the solitary and more completely social members of the Vespidæ. The observations of F. X. Williams, conducted in the Philippines, concern the genus *Stenogaster* which comprises both solitary and social species. They live in shady forests where they construct small fragile nests (Fig. 6) composed of rotten wood or soil, often attached to rocks or vegetation. Each nest consists of a small number of cells (Fig. 6) and a colony comprises only a few individual wasps. The female parent exhibits what has been

termed *progressive provisioning* in that she feeds the larvæ daily until they are fully grown, when the cells are sealed over. Upon emergence from the pupæ the daughter wasps share the nest with the parent.

FIG. 6.—Suspended Nest of Seven Cells of a Wasp of the Genus *Stenogaster* (Philippine Islands)
After F. X. Williams.

The Epiponinæ are the largest subfamily of social wasps: they are widely distributed in the tropics but mainly developed in South America. All the species are social and among the most primitive are African forms belonging to the genus *Belonogaster*. Their nests are of larger dimensions than in the preceding group, and may comprise up to about 300 cells composed of masticated wood or, as it is often termed, 'wasp paper'. The female parent feeds the larvæ with portions of malaxated caterpillars and, according to E. Roubaud, she is often joined by others who form a combined nest. In the stronger colonies the beginnings of a division of labour are betrayed in that the newly emerged females devote themselves to tending the brood; as they become older they become active in foraging for prey and nest-building material, while the oldest individuals give themselves over to egg-laying. The males behave like parasites; they do not desert the comb, and take whatever food they can secure. When the colony becomes very numerous, the females leave it in small companies and found new colonies elsewhere. In some of the South American members of the subfamily social life attains a higher degree of development in that the female members of a colony are not all alike. A certain number of the individuals are fertile forms, with well-developed ovaries, and capable of fecundation—they are in fact '*queens*'. Others have imperfectly developed ovaries, and are consequently either sterile or only capable of laying unfertilized male-producing eggs. Not very much is known of the behaviour of these two kinds of females, but the last mentioned form a caste termed the *worker*. Since these colonies are perennial, and have numerous queens, they tend to assume a large size with a population comprising several thousand individuals. The overcrowding which results is relieved by their

periodically emitting swarms of workers, together with a small number of the queens. Such swarms are the fore-runners of new colonies since they settle down and begin nest-building on their own account. Swarming, it may be added, is unknown in wasps outside the tropics.

The Ropalidinæ are a small group found in the tropics of the Old World. In *Ropalidia* we have a more primitive social organization more nearly like that of *Belonogaster*. The colonies comprise a small number of functional females and, according to Roubaud, workers also. The latter, however, are much less numerous. Swarming apparently occurs in some of the species.

The Polistinæ are nearly world-wide in their range of distribution. Members of the genus *Polistes* are the light yellow, rather slenderly built wasps that are familiar objects, for example, in southern Europe, India and North America. As in the preceding groups, the comb is not covered by any protecting envelope. It is formed of papery material and is suspended by means of a pedicel from beneath eaves, rafters, ceilings or even stones or bushes. The beginnings of the combs are the work of a single queen, but the cells are added to by the conjoint labours of her progeny which includes a certain number of workers. Young fertile females are produced towards the end of the summer and, after fecundation, they hibernate individually, and in the following spring found new colonies. This, very briefly, is what occurs in temperate lands where the colonies are annual associations only. In tropical countries the colonies tend to be polygynous or, in other words, they are founded by a number of queens. The warm equable climate coupled with a sufficiency of food at all times of the year, fosters the survival of the colonies from year to year. Unlike species found in temperate regions, certain of the tropical forms periodically give off swarms.

The Vespinæ include the largest and most characteristic of the social wasps and the genus *Vespa*, along with *Polistes*, are the only wasps of social habits that occur in the north temperate zone. Species of the first mentioned genus are the familiar wasps in Britain where, it may be added, *Polistes* is not found. The species of *Vespa* are monogynous, each nest being founded by a single fecundated queen. The material, or wasp paper, used in its construction consists of weather-worn but sound wood, particles of which are rasped off palings, fences, dead trees, etc., by means of the mandibles: they are worked up with the aid of saliva and masticated to form a substance which, when dry, has a paper-like consistency. The comb, when first formed, consists of a tiny group of cells suspended by a central pedicel. Very soon a more or less umbrella-like envelôpe is formed over it. New cells are added at the periphery of those already formed and, when one horizontal layer of comb has attained a suitable size, new tiers are built below and interconnected by means of vertical pillars. This goes on until about seven or more combs are constructed and, at the same time, the envelope is added to in order to keep pace with their growth (Fig. 7). When the nest is fully formed it is spheroidal, when viewed from the outside, and it is invested by several layers of coverings which protect it from rain and also serve to maintain a more or less equable temperature within. The individual cells are hexagonal in form, open below and closed above. The queen deposits an egg in the angle of each cell, nearest the centre of the comb, affixing it in position by an adhesive secretion. In a few days, according to the temperature, the larvæ hatch and are fed by the queen, mainly upon masticated portions of insects, until they are ready to pupate. Prior to transforming into the pupa, the larva spins a cocoon within the cell and

closes the mouth of the latter with a floor of tough silk. After a period of four to six weeks from the time of oviposition, the fully formed wasps bite their way through the floors of the cells and emerge. These indi-

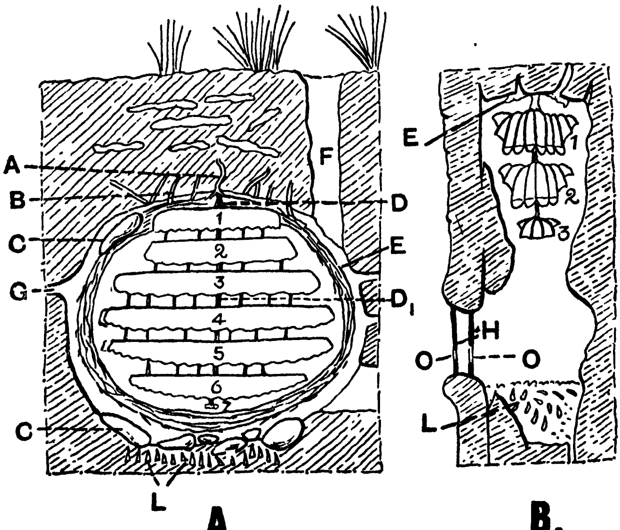


FIG. 7.—**A.** Section of Subterranean Nest of *Vespa germanica*; **B.** Section of Nest of *Vespa crabro* in a Tree Hollow

A, root to which first attachment *D* was made; *B*, secondary attachment; *C*, pieces of flint; D_1, suspensory pillar; *E*, envelope, in **B** its vestiges; *F*, entrance; *G*, side gallery; *H*, lamellæ closing opening to tree hollow; *O*, entrance orifices in lamellæ; *L*, saprophagous dipterous larvæ. The numerals refer to layers of comb in order of construction. Adapted from Janet.

viduals are always workers and, very soon, the entire care of the young and the extension and completion of the nest is taken over by them, the parent then devoting herself to egg-laying. Towards the end of summer

larger cells are constructed and these 'royal' cells are destined for the females or queens of the following year. The fertilized eggs produce either females or workers depending upon the nutritional treatment the larvæ receive. Males are also produced late in the season and arise from unfertilized eggs either laid by the queen, or by certain of the workers who have undergone increased development. After coition the daughter queens leave the nest and hibernate each in a favourable, concealed situation. These are the foundresses of the colonies of the next year. The old colony becomes derelict in autumn when the workers and males gradually perish.

This brief account of the characteristic features of the habits in the five subfamilies of social wasps will enable us to pass on and consider the subject from a more general standpoint.

The feeding of the larvæ on a carnivorous diet is clearly inherited from the solitary wasps among which the habit is almost universal. In the solitary species mass provisioning is the rule: one or more immobilized insects are provided by the parent, and the cell closed down. Among the social species progressive provisioning prevails and, in most cases, not whole insects, but premasticated portions of insects are supplied to the brood from time to time. The hungry, eyeless larvæ raise their heads at the approach of food, perhaps in response to some odour stimulus. It is now established that the activities of the attendant wasps are by no means 'disinterested' and, in return for the food supplied to the larvæ, the wasps themselves eagerly imbibe saliva as it is emitted from the mouths of their young. They, in fact, stimulate its flow either by contact or even by seizure of the heads of the larvæ by means of their mandibles, should the desired secretion not be forthcoming. This reciprocal feeding is termed 'trophal-

laxis' and, as will be seen later, is of very general significance in the behaviour of social insects. Sometimes the saliva is demanded without any reciprocal exchange in nutriment; male wasps, for example, may exploit the brood and give nothing in return. There are times also when the larval secretion is exploited out of all proportion to the amount of solid food rendered by way of compensation. It follows, therefore, that an avidity for these larval secretions, rather than maternal solicitude, initiates and maintains the bond between social Hymenoptera and their young.

It would appear that trophallaxis in wasps has a direct bearing upon the occurrence of the worker caste. Owing to the expenditure of saliva by the larvæ, and the numbers which are simultaneously reared, many are inadequately nourished and pupate as small individuals with imperfectly developed reproductive organs. In this manner it is claimed the workers are produced. The exigencies of collecting food for a numerous hungry brood and of maintaining and extending the nest, is exhausting labour, which tends to keep the workers sterile. It is only later in the season that the abundance of workers, and the amount of food brought in, allow of the larvæ being more copiously fed. Many develop in consequence into fertile male-producing (parthenogenetic) individuals, while others, more intensively fed, become the future queens, which are capable of fecundation and give rise to females. The arrestation of the development of the ovaries or their functional atrophy in the workers, induced by the causes just mentioned, has been termed by the French entomologist, Paul Marchal, 'nutricial' castration. He showed that, if artificial means be taken to reduce or prevent the brood-care function, the workers appropriate the food which, under ordinary circumstances, would be given to the larvæ.

Under such conditions as many as one-third of the members of the caste may become fertile and lay male-producing eggs.

The evolution of the worker has not progressed very far among wasps. In some of the species of Epiponinæ the caste is undifferentiated, as regards external characters, from the queens : only dissection of the reproductive system can determine whether a given individual is a worker or not. Among the Ropalidinæ and Polistinæ external differences are so slight as to demand close examination. In the Vespinæ, however, differentiation in the two cases becomes distinct. The constant smaller stature of the workers, along with certain colour differences, renders their identification a simple matter. Among wasps, however, differentiation of special caste structure in relation to function has not been evolved.

The conditions of social development which involve either polygyny or monogyny, as the case may be, are by no means apparent but are fundamental in so far as our subject is concerned. It will become increasingly evident, when discussing other groups of social insects, that monogyny, which involves the concentration of the reproductive function in a single individual female of enhanced fecundity, appears, on the face of it, to be precarious for racial survival. This raises speculation respecting the directive or selective influences that have invoked its development. Certain eminent authorities regard polygyny as the more primitive of the two phases. If we exclude such a rudimentary grade of social organization as prevails in *Stenogaster*, where a single female initiates the incipient colony, polygyny is confined to wasps inhabiting the tropics or subtropics. It is probable that the social habit arose in the first instance in such regions, and the species, as they extended their range into temperate lands, became subjected to cor-

related modifications in their social organization. From what has already been explained it will be apparent that we might arrange the social wasps in the following series.

1. In *Belonogaster* several females, most likely sisters in origin, take part in the foundation of the colony.

2. In certain genera of the Epiponinæ the females are differentiated into sexually functional queens and sterile, or only male-producing, workers. The initiation of new colonies is the combined effort of a small band of individuals, consisting of queens and workers, which have issued as a swarm from the parent colony.

3. In temperate regions we find, in both *Vespa* and *Polistes*, that the colony is founded by and 'presided over' by a single queen, while the workers only develop subsequently. It would thus appear that, among wasps, monogyny has resulted as a later specialized development. The phenomenon is the prevailing one in temperate zones where climatic inclemencies result in the ultimate dissolution of the original colony. The sole survivors are the young fecundated queens who disperse in order to hibernate in more favourable quarters. It may be argued that, if conditions had been favourable, the young queens would have remained in the original nest and subsequently founded polygynous colonies, as in the tropics.

Following this sketch of the evolution of social organization among wasps, we may proceed to consider the same subject with respect to bees.

CHAPTER IV

SOCIAL BEES

BEES comprise an even larger number of species than wasps and, contrary to popular belief, an overwhelming majority are solitary in behaviour. Scarcely five per cent. of the known species are social insects. As a group, bees are to be regarded as specially differentiated wasps which have forsaken carnivorous habits and resorted to feeding upon pollen and nectar. In order to procure these necessaries of life they have become highly adapted in various ways for visiting and exploiting flowers: the expression 'blumenvespen', used by some German writers, expresses this fact.

Structurally bees have much in common with solitary wasps of the Sphecoid group and one authority has gone so far as to unite them in a single common series. Without subscribing to this rather extreme view, it is necessary to point out that hard and fast distinctions are by no means easy to draw. In bees, however, the tarsi of the hind legs are dilated or thickened and the body pubescence comprises branched or plumose hairs. Their most obvious distinctions lie, however, in structural adaptations for collecting nectar and pollen and for comb-building.

The mouth-parts have well-developed mandibles, while the maxillæ and labium are specially modified for the sucking or lapping of nectar. The more primitive bees, which visit flowers with exposed nectaries, have

the maxillæ and labium short as in wasps, but in the social and other specialized forms, which resort to flowers with deeply-seated, concealed nectaries, these same organs are greatly elongated, the labium being drawn out to form the so-called tongue. The under surface of the latter is provided with a channel so overlapped by special hairs as to form practically a closed tube. Along this passage nectar is sucked into the pharynx whence it passes into the crop or storage chamber. Here it becomes mixed with an enzyme, presumably derived from the salivary glands which converts its cane-sugar into invert sugar (dextrose and levulose), which does not require hydrolysis before being capable of absorption. In this changed condition the nectar becomes honey and it is regurgitated to be supplied as food for the brood. The adaptations for collecting pollen are also pronounced: the hairy body, always clothed with at least some admixture of plumose hairs, serves to retain the pollen grains until the insect combs them off by means of its legs. The pollen becomes collected in masses and attached either to the ventral aspect of the abdomen where there are special hairs for retaining it: or, to the broadened outer surfaces of the tibiæ and tarsi of the hind legs. Another important feature is the production of wax, all social bees utilizing this material for comb-building. It is delivered as a secretion discharged from glands located between the abdominal segments where it becomes hardened into lamellæ. Among certain exceptional bees these special adaptations are not developed. In the primitive members of the genus *Prosopis* the pollen is swallowed as well as the nectar and consequently corbiculæ, or special areas of the body for retaining this material, are wanting. Special adaptations are likewise absent in parasitic bees living at the expense of other species.

When we pause to consider the social behaviour and organization of bees we find a remarkable parallelism between these insects and wasps. They express themselves in a somewhat different way but, nevertheless, evolution from the solitary species through the subsocial to the most perfectly social forms can be traced. Solitary bees practise mass provisioning: each cell is adequately provisioned, an egg is laid therein and the receptacle finally closed without the parent having any further concern with the offspring. In the family Andrenidæ, among certain species of the genus *Halictus*, the parent survives the development of her progeny and betrays some concern for its welfare. In *H. quadricinctus*, Verhoeff found that the nest of this solitary bee is a rude comb of about sixteen to twenty cells which are lodged in an underground chamber. The cells are progressively provisioned and finally closed, but the parent guards the nest and may survive until the young bees emerge. Thus there is an actual, although brief, contact of parent and offspring and an advance over the mere mass provisioning of other solitary bees. With the species *H. malachurus* the observations of Stöckhert have shown that a definite advance in social evolution has taken place. The overwintered females commence to build cells in spring and lay their eggs. About mid-June the progeny emerges and it consists of a smaller type of bee than the parent with different cuticular sculpturation. These individuals have been regarded by taxonomists as a separate species, *H. longulus*; all are females, no males being known. The original parent still survives and her progeny remain in association with her: they build new cells and collect pollen for their provisioning. Fresh progeny of the *longulus* type are produced and it is not until the month of August that true *malachurus* individuals appear. A little later

malachurus males also develop : they pair with females of the same type but exhibit no concern for the *longulus* females. Towards the end of the season the original *malachurus* parent dies, together with the males and the *longulus* females. The young fecundated *malachurus* females, on the other hand, hibernate in the parental nests and give rise to the next year's cycle of individuals. The *longulus* females are infertile and dissection has shown that they are never fecundated : they are, in fact, workers. Several other species of the genus *Halictus* exhibit a similar differentiation of life cycle and we have in these examples a rudimentary but true social life. As will be seen later, it closely foreshadows that which prevails in the Bombidæ or bumble bees rather than in the hive bee.

The family Andrenidæ is not the only one among bees which includes both solitary and social species. Phenomena of a similar kind occur in the genus *Allodape* of South Africa which belongs to the family Ceratinidæ. This latter family, however, is only distantly related to the Andrenidæ and the rudimentary social life exhibited among certain of its species is clearly an independent development. The economy of species of *Allodape* has been recently investigated by H. Brauns. It appears that the parent female builds no cells at all, but merely excavates a tunnel in the stem of some suitable plant possessing a soft pith that can be easily excavated. In this tunnel the eggs are deposited, one below the other in a tier, the oldest being at the top. The parent feeds the larvæ, in some species by mass provisioning, in others by the progressive method. All the female progeny, so far as is known, are fertile and they share the business of egg-laying and provisioning. It will be noted, therefore, that this genus is more primitive than *Halictus* in several ways. The nest, for instance, is of a most rudi-

mentary character: there is no worker caste and the colonies are to a large extent polygynous, although a single female may initiate the foundation of each nest in the first instance.

Apart from the two exceptions briefly mentioned, all social bees are members of the families Bombidæ and Apidæ: in these two groups there are no solitary species at all. The Bombidæ include about 200 species which largely inhabit temperate lands and the mountains in tropical countries. Their social organization closely resembles that found in *Vespa* and in certain species of *Halictus* and, in the north temperate zone, the colony is an annual one. Its foundation is initiated by a single fertilized queen which has overwintered in a manner already explained in the case of *Vespa*. In the genus *Bombus* a worker caste is present, as in the two genera mentioned, and the external structural differences between the workers and the queens manifest themselves similarly in the size of the respective individuals. The workers are incapable of being fecundated and such parthenogenetic eggs, as they may produce, develop into male bees. On the advent of mild weather in the spring the hibernated young queens become roused from their winter lethargy and seek out situations for their future nests. The actual nest itself commonly consists of fine grass or fragments of moss which are formed into a hollow ball and placed deeply in the ground: certain species of the genus, known as carder bees, construct surface nests concealed among the ground herbage. Having constructed the nest the queen then proceeds to accumulate pollen which is mixed with honey until it assumes a paste-like consistency. After placing a mass of this material in the nest, she constructs a circular wall of wax on the top of it and, in the cell thus formed, the first batch of eggs is deposited and the cell then

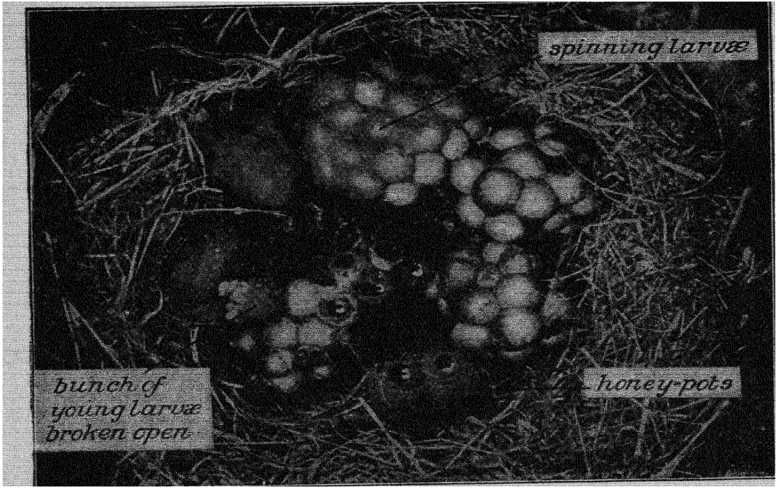


Fig. 8.—Nest of *Bombus lapidarius*
***After* Sladen.**

sealed down. The wax, it may be added, is secreted (by the queens and the workers) beneath the dorsal and ventral shields of the second to fifth abdominal segments, and is often used with some admixture of pollen. The queen also constructs a receptacle or so-called 'honey pot' which she fills with honey to form a food reserve for her own consumption during the time she is brooding over the eggs (Fig. 8). The larvæ hatch in about four days and feed on their prepared bed of pollen paste. Up to this stage the parent bee behaves very much after the manner of a solitary species. A significant change, however, now comes about. She gnaws a hole in the roof of the cell and, by regularly supplying her brood with regurgitated honey and pollen, she thus adopts progressive provisioning. On about the twenty-second or twenty-third day after oviposition the first workers commence to appear. New cells become added to the colony, each containing about one dozen eggs, and, when sufficient numbers of workers have emerged, the duties of provisioning devolve upon them. Once this has happened the queen becomes confined to the nest. The workers construct further receptacles for both honey and pollen, additional new cells are formed and the colony, when it attains its maximum strength, contains from about 100 to 500 bees. Later on in the season certain of the larvæ, derived from fertilized eggs and enclosed in the larger cells, are abundantly fed and develop into new queens which subsequently hibernate. These are fertilized, it may be added, by males which appear about the same time. There appears to be no evidence that special food plays any part in queen production, as happens in the case of the hive bee, and the differences between the queens and workers are attributed to the quantity rather than the quality of the food which they receive. The size differences between these

two types of female individuals are by no means so constant as in *Vespa*: these differences are often not clearly marked owing to the prevalence of transitional series between the smallest workers and the less robust queens. Gradations of this kind may be observed within the confines of a single nest.

While the *Bombus* colonies in temperate climates are annual developments only, accompanied by monogyny, it is noteworthy, just as in wasps, that in certain Neotropical species the colonies are perennial and polygynous and multiply by swarming.

The family Apidæ comprises two subfamilies—the Meliponinæ, including the genera *Melipona* and *Trigona*, and the Apinæ which are represented by the single genus *Apis*. The Meliponinæ number about 250 species which are largely centred in the tropics of South America, with relatively few representatives in the fauna of the Old World. They comprise the smallest of all bees: in some of the species the individuals measure less than 3 mm. in length, but their diminutive size is counterbalanced by their numerical dominance. Although frequently termed stingless bees this name is misapplied, since a vestigial sting is present. On account of their small size they are sometimes called mosquito bees, and when disturbed these individuals may literally swarm over the face and in the hair and nostrils of a human intruder, to his very evident annoyance and discomfort. The nests are found in tree hollows or in branches: less frequently they occur in the ground or in termites' nests. Most species mix their wax with earth or other material so as to produce a brown or black substance termed cerumen, which is used for comb-building. The wax is secreted between the dorsal shields of the second to fourth abdominal segments and is produced by the queens, workers, and males, and, in these respects, the

Meliponinæ are unique among bees. The nest consists of a compartment containing the brood which is separated off from the stores of honey and pollen. The entrance usually projects as a conspicuous funnel which is often guarded by the workers by day and may be even closed up by means of cerumen each night. Caste differentiation is well marked in these bees and the queens differ from the workers in certain notable structural characters. The head is smaller and the abdomen more voluminous while the whole body is more hairy; also, the tibiæ and tarsi of the hind legs are altered in character so as to be useless for pollen-collecting. The worker, apart from her sterility, retains the secondary characters associated with the duties of her sex: she is, in fact, the typical female, morphologically, while the queen has undergone degeneration. This change in her structure is correlated with the fact that, although the colonies are monogynous, swarms are èmitted when daughter queens, accompanied by detachments of workers, leave the parent nest and found new colonies. Since the queens are restricted to reproduction, organs employed in pollen-collecting, being no longer required, disappear. The provisioning of the brood cells is by the mass method, as among solitary bees, and in this respect the Meliponinæ are unique among social insects. There appears to be no qualitative difference in the dietary regime of the queen as compared with the workers, and in some species she is reared in cells of similar form and dimensions. The males are unique in their behaviour since they partake in the work of comb-building and are consequently by no means an unproductive drain upon the resources of the colony.

In the family Apidæ social organization among bees attains its highest phase of development. The single genus *Apis* comprises but four species, viz., *A. mellifica*,

the common hive-bee, together with the oriental species *dorsata*, *indica* and *florea*. The largest and most primitive of these species is *Apis dorsata* which forms large and massive, naked combs suspended from branches, rocks or buildings. It selects a locality where suitable flowers afford abundant supplies of nectar and, after these have ceased to bloom, the whole colony migrates to another situation and there constructs a new comb. On account of its nomadic life it has not been possible to establish this species of bee in apiaries. In this species the queens, drones, and workers are all reared in cells of the same size and of similar form. *Apis florea* is the smallest member of the genus : in certain respects it is intermediate in its characters and behaviour between *A. dorsata* and *A. indica* and *A. mellifica*. As in *dorsata* it constructs a naked pendent comb but the cells are specially differentiated, as in *A. indica* and *A. mellifica*, according to whether they are destined to contain queens, workers or drones. *A. mellifica* and *A. indica* are so closely related that doubts have been raised with respect to their specific distinction, and it is possible that the latter is merely a subspecies of the former. They both nest in hollow cavities, especially those in tree trunks, or they may resort to buildings or caverns. The common hive bee in the absence of a hive will resort to hollow trees.

The literature on the hive bee (*Apis mellifica*) is enormous and, as the chief facts respecting its habits are well known and easily accessible to all readers, only certain features require discussion here. The queen, apart from her notably longer abdomen, is distinguishable from the workers by the complete loss of the pollen-collecting apparatus on the hind legs : she bears no wax glands : the ligula and sting are shorter, the brain is smaller, there are many fewer placoid sensillæ on the antennæ,

and pharyngeal salivary glands are absent. She is, in fact, a highly specialized egg-laying machine and is degenerate with respect to other characters common to the queens of more primitive bees. As in the other social Hymenoptera, already discussed, the fertilized eggs produce either queens or workers and the unfertilized eggs give rise to drones parthenogenetically. Two polar bodies are given off irrespective of whether

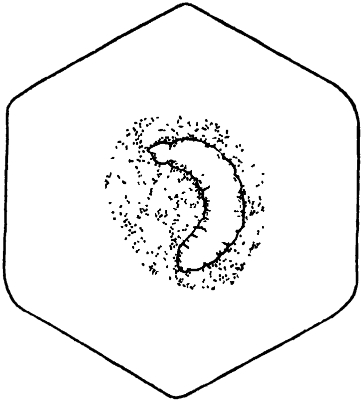


FIG. 9.—Larva of Hive Bee, one day old, lying in Centre of the Base of its Cell in a Mass of 'Royal Jelly'

After J. A Nelson and A. P. Sturtevant, *Bull.* 1222, *U.S. Dept. Agric.*

the eggs are fertilized or not. The somatic number of chromosomes is 32 in the female castes, but in the drones these elements are haploid (16). No reduction division takes place during spermatogenesis and consequently 16 chromosomes enter each spermatozoon. The young larvæ are at first uniformly nourished upon a special nutrient material termed 'royal jelly' produced as a secretion of the lateral pharyngeal glands of the worker bees (Fig. 9). Larvæ destined to produce queens are fed with this substance throughout their lives, while the drone and worker larvæ receive a different diet from the fourth day onwards. Their food no

longer consists of royal jelly but is composed of a mixture of honey and predigested pollen.

Von Planta has determined the composition of the royal jelly and his results (which are given in percentages of the dry weight) have been widely accepted. It will be seen from the accompanying table that the composition of the royal jelly appears to differ in the proportions of its main constituents according to the type of larvæ it is being fed to.

COMPOSITION OF LARVAL FOODS ACCORDING TO VON PLANTA

	Queen Larvæ.	Drone Larvæ.			Worker Larvæ.		
	Percentages of Dried Substance (Average).	Under 4 Days.	Over 4 Days.	Average.	Under 4 Days.	Over 4 Days.	Average.
Proteid	43·14	55·91	31·67	43·79	53·38	27·87	40·62
Fat .	13·55	11·90	4·74	8·32	8·38	3·69	6·03
Sugar	20·39	9·57	38·49	24·03	18·09	44·93	31·51

Elser has recently (1929) re-investigated its composition as found in the royal cells by means of up-to-date microchemical technique. He finds that its chemical nature is tolerably constant and that its *p*H is on the acid side. Elser's determinations differ in certain respects from those of von Planta, more especially with regard to the proportions of sugar and proteid present. In Fig. 10 his conclusions are schematized and the proportions of its constituents with respect to total weight (not dry weight) are represented. The sugar, it may be added, consists of invert sugar only. Von Planta's claim, that the early food of the drones and workers differ notably with regard to the proportions of sugar and fat present, is not upheld by the more recent work of Koehler, whose analyses showed no significant differ-

ences in the two cases. Koehler was unable, owing to lack of sufficient material, to extend his analyses to the material supplied to the queen larvæ. It cannot be regarded, however, as being definitely settled that the royal jelly as supplied to the queen larvæ differs significantly from that given to the workers and the drones. From the fourth day onwards, however, the regime undergoes very definite alteration as has been already mentioned. That this difference in nutrition is responsible for determining whether a given larva grows up

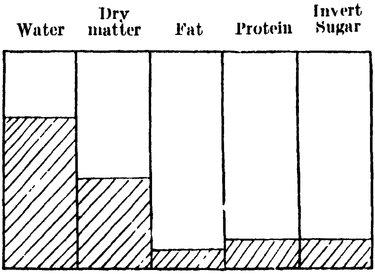


FIG. 10.—Diagram showing the Composition of the 'Royal Jelly'
From Elser.

into a queen or a worker, is proved by the experiment of transferring either the eggs or the newly emerged larvæ, from worker to queen cells or the reverse. It would seem, therefore, as if the royal jelly contains some essential accessory food substance, not present in honey and pollen, which, when given throughout the larval life, becomes the determining factor in inducing the morphological differences that result. The whole of the interior economy of the hive, and comb-building, devolves upon the workers with the exception of the maintenance of the species. At times, however, fertile workers may

develop but their progeny consists only of parthenogenetically produced males. The observations made in Germany by G. A. Rösch, during the last few years, point to the conclusion that each worker bee is able to undertake all the duties that present themselves. These duties, he claims, follow a definite sequence in time and each bee, of a given age, performs the same specific functions. It will be evident, therefore, that there is specialization of labour among the workers in relation to their age and not, as in ants, in accordance with morphological differences in their body-structure. A useful summary of Rösch's work is given by D. M. T. Morland whose paper[1] has been consulted in preparing the present account. The life of the worker bee may be divided into three periods as follows:

First Period. The newly hatched bees prepare cells for the reception of the future eggs and also help in maintaining the right temperature of the hive. After the second day, feeding of the older larvæ with honey and pollen is taken over, and this goes on until the sixth day. From the sixth, until about the fifteenth day, the pharyngeal glands are functionally active and the bees consequently devote themselves to feeding the very young larvæ. By the end of this time the pharyngeal glands tend to atrophy and brood-feeding ceases.

Second Period. This is inaugurated with the first flight from the hive, the so-called orientation flight. During this period the bees receive and store nectar from foraging bees: they attend to the pollen brought in, and act as general workers in the hive. Bees of this age have their wax glands in the active secretory phase and whatever comb-building that

[1] *Annals of Applied Biology*, Vol. XVII, 1930. pp. 139–49.

may be required is carried out at this time. Towards the close of this period, which lasts for about 10 days, the bees may take on the function of guarding the hive entrance.

Third Period. In this period, which is from 20 to 30 days' duration, the workers are active only in the field and are engaged in foraging for water, pollen, nectar and propolis. They continue at this kind of work until they die.

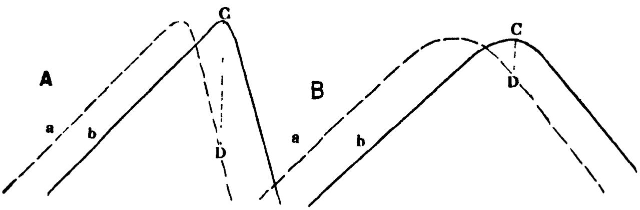


FIG. 11.—Diagram showing relation of Brood Curve *a* and Curve *b* of Worker Bees in the First Period of their Life when the Pharyngeal Glands are most active

In A a rapid fall in egg-production leads to a surplus of bees (C–D) in this stage, thus giving rise to a tendency to swarm. In B the brood curve is less steep and gradually falls away from a maximum. In this case the surplus of bees (C–D) is much less and the tendency to swarming is consequently almost eliminated. The distance between *a* and *b* represents the period taken by the workers in developing from the egg to the brood-feeding stage of their life. Adapted from Morland.

Whether the sequence of duties during each period is exactly as described further observation alone can determine, but the main point is that, since fresh bees hatch from the cells successively, there is always a number of them of different ages occupied on different duties. Moreover, the division of labour is flexible, and Rösch states that special circumstances may demand functions to be carried out by the workers which they would not normally do until a later period. He further claims

that when there is a prevalence of a larger number of workers, in the first period of their life when the pharyngeal glands are most active, than brood attention demands, a surplus of their secretion supervenes. This leads to the construction of an excess of queen cells which will contain larvæ capable of absorbing relatively large amounts of the glandular product. The construction of these cells marks the advent of swarming (Fig. 11) and, when the latter event takes place, the old queen leaves the hive accompanied by a host of workers. Of the daughter queens that issue from the cells one takes the place of the original queen. She takes an aerial flight at the first opportunity and is followed by a number of drones: mating supervenes in mid-air and the fertilized queen then returns to the nest. If a second swarm be emitted the same season it is accompanied not by the reigning queen, but by a newly emerged virgin individual. As is well known, the colonies of the hive bee are perennial and a flourishing hive will contain 50,000 to 80,000 bees, the vast majority of them being workers. A queen may live for several successive years, and is capable of producing up to about 1,500,000 eggs during her existence.

Social life among bees appears to obtain without that peculiar interchange of nutriment between the workers and larvæ, which is so prevalent among social wasps. Whether we can dismiss all possibility of the occurrence of trophallaxis is a moot point. In this connexion it is noteworthy that an American observer, B. Lineburg, has commented upon the excessive amount of time nurse bees devote to visiting the cells of the older worker larvæ. The food which these larvæ receive does not appear to be of a character requiring much preliminary elaboration on the part of the workers. It is, consequently, difficult to explain the amount of time spent

by such bees in the cells merely on the assumption that the larvæ are being fed by them throughout that period. Apart from the mere raising of this problem there is little more that can be said upon the subject.

The main features respecting the grading of social organization, as exhibited among bees, may be recapitulated as follows :

(*a*) In *Allodape* the colonies are to a large extent polygynous although their initiation may be the work of single females. There is no worker caste and the nest is of a very rudimentary nature.

(*b*) In *Melipona* and *Trigona*, and certain tropical species of *Bombus*, the colonies are polygynous and a worker caste is present New colonies are founded by a single fecundated queen, together with a number of sister workers. The nest is of more elaborate construction and the comb is composed of wax admixed with foreign material.

(*c*) In most species of *Bombus* the colonies are monogynous for a large part of their life. They are annual affairs only, swarming does not prevail, and the new colonies are founded by single fecundated queens. The worker caste is not sharply demarcated from the queen.

(*d*) In *Apis mellifica* the colonies are monogynous throughout their existence. They are perennial and the new colonies are founded by a single queen accompanied by a number of daughter workers. The queen is highly specialized for reproduction, and, since the ancestral female secondary characters are only retained by the workers, the two types of female become sharply differentiated. The nest consists of an elaborate comb constructed of pure wax.

CHAPTER V

ANTS AND POLYMORPHISM

SOCIAL life among insects attains its highest evolutionary development in ants. Structurally, ants are easily recognized by their elbowed antennæ and by the pronounced constriction of the abdomen near its junction with the thorax. With certain exceptions, to be mentioned later, ants differ from all other social Hymenoptera in being wingless and, it may be added, all the species are social in habit. They form a single vast family comprising about 3,500 described species.

Ant societies inhabit very diverse kinds of nests. Many species construct their abodes in the soil, the galleries and chambers being excavated under ground. Perhaps the largest number of kinds merely hollow out the ground beneath stones or logs which serve as protective coverings. Other species form mound nests which may be constructed not only of excavated soil, but also of heaped up masses of straws, pine-needles, twigs, leaves or other materials within which a series of galleries and chambers are constructed. In tropical countries many species take advantage of cavities occurring in stems, petioles, thorns, bulbs, etc.: others construct suspended nests attached to trees and formed of earth, carton or silk. The tropical tree ant, *Œcophylla smaragdina*, forms leaf nests, the leaves being bound together by means of silken threads. Doflein, and later observers, have shown that the silk is provided by the

larvæ which are held in the jaws of the workers and used, as it were, like shuttles in that they provide the silk which fastens the leaves together.

The normal male and female ants are winged with well-developed eyes. The male is smaller and more slender than the female : the head is proportionately smaller, the eyes are more highly developed, the mandibles are weaker and the antennæ often longer and more delicate. Individuals of the two sexes may be very differently coloured, the male being sometimes yellow or red and the female black. It is evident, therefore, that the male bears a much less close resemblance to the female than among bees and wasps. In some species both winged and wingless males may be present, the apterous individuals bearing a marked resemblance to the workers. Wingless females also occur in some ants and they may be the only type present, while, among others, both apterous and alate females prevail.

At certain times of the year, differing for various species, the winged males and females leave the parental nest in large numbers. These nuptial flights may affect a considerable area of country simultaneously owing to a number of colonies of the same (and often of different) species being affected at the same time. In this manner dissemination of the species is provided for, since the fertilized females usually found their colonies some distance from those wherein they originated. Mating of the sexes often occurs in the air and may take place between brothers and sisters or with individuals from different colonies. Under ordinary circumstances the fecundated females, or queens, found new colonies in much the same general manner as in *Bombus* or in *Vespa*. The young queen descends into the ground and, having rid herself of her now useless wings, seeks out some convenient cavity or excavates a cell in the earth. She

then closes the opening and thus remains entombed while her eggs undergo development. The voluminous wing-muscles, being no longer functional, degenerate and the disintegration-products pass into the blood plasma. The latter thus becomes charged with nutritive material which serves to build up the yolk in the developing eggs. In due course the first batch of eggs is laid, and the queen feeds the larvæ with her saliva until they pupate. The first individuals to appear are workers, and these soon take over the charge of the colony, feeding the queen and themselves besides tending the brood. The parent is thus freed to devote herself exclusively to the business of oviposition. In many ants the mated females return to their original nest and increase its population. When the original colony becomes overcrowded some of the queens, accompanied by workers, leave the nest to form a new society on their own account. This habit, which is comparable with swarming in wasps and bees, is very prevalent among the Doryline ants of the tropics.

Excepting parasitic species, which will be dealt with in a subsequent chapter, all ants possess a well-differentiated worker caste composed of apterous individuals. As in other social Hymenoptera they are, normally, sterile females. They may be distinguished from deälated queens by the more simply constructed thorax, the smaller eyes, while the ocelli are reduced or often wanting: also, the inflated hind-body or gaster is much less pronounced in its development. In certain subfamilies of ants the workers are monomorphic, but in others polymorphism prevails. In the latter instances a graded series of individuals is present: at the one extreme are large-headed forms, approaching the queen in stature, and at the other extreme are very small individuals. The members of such a series exhibit, not

only morphological, but also functional differences. The largest examples commonly act as defenders of the

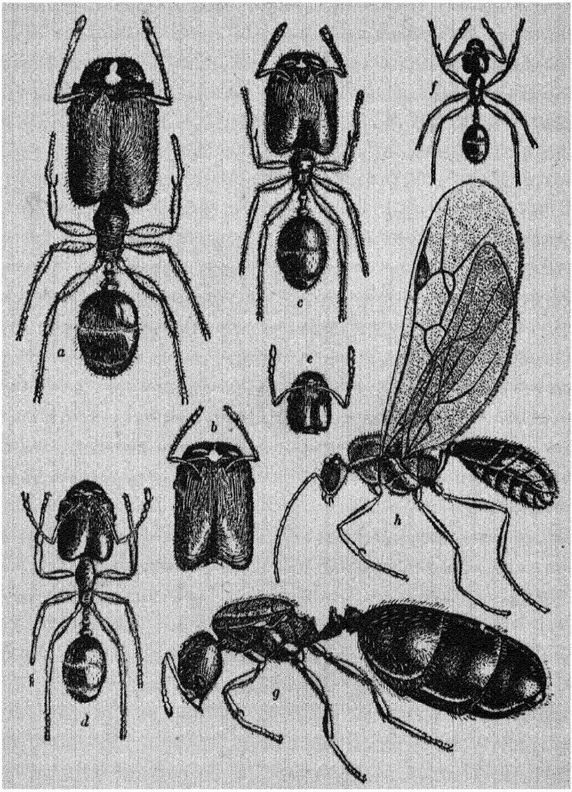


FIG. 12.—*Pheidole instabilis*

a, soldier; *b–e*, intermediate workers; *f*, typical worker (micrergate); *g*, deälated queen; *h*, male. *After* Wheeler.

colony and in some species they use their powerful mandibles for crushing seeds or the hard parts of their

insect prey. The smaller workers in the same series tend the brood, forage for food, engage in nest-building or in the cultivation of fungus beds. There are other species of ants in which only the two extreme types of worker occur, the large forms being termed soldiers and the small individuals are the true workers (Fig. 12). Again there are species in which the soldier caste has disappeared and only the small workers remain. Polymorphism, therefore, undergoes many phases in ants; in fact no less than twenty-one different forms have been recognized in these insects. Among them, eight of the forms are due to pathological causes, while the remainder are special developments of the male, female, soldier, or worker. In some species of ants the queen has disappeared and her place is taken by a gynæcoid or egg-laying worker capable of mating with the male. In other cases a colony may lose its queen and one or more workers develop into egg-laying substitute queens. While ordinary unfecundated workers are occasionally fertile and their eggs develop, as would be expected, into males, there is evidence that this is no invariable rule. A number of observers including Reichenbach, Tanner, Comstock, Crawley and Donisthorpe have recorded instances which seem only to point to the conclusion that unfertilized worker eggs have developed into other workers.

The feeding habits of ants are not only very varied but also attain considerable complexity. It is remarkable, as Wheeler points out, that hunting, pastoral and agricultural modes of life appear to have succeeded one another in these insects in the same sequence as they are believed to have done in the case of man. All the most primitive ants are carnivorous or, in other words, hunters of various kinds of insect life. This habit is betrayed particularly well in the tropical 'legionary'

or 'driver' ants of the subfamily Dorylinæ, which do not construct permanent nests, but lead a nomadic life wandering from place to place. The workers are polymorphic, varying from large soldiers with powerful dentate mandibles, through intermediates, to very small true workers or micrergates. Although blind, the other sense organs of these forms are well developed, and they make sorties for predatory purposes, attacking and seizing other insects or spiders, etc., which they carry off to the nest.

There are other groups of ants which live mainly upon saccharine matter obtained partly from extra-floral nectaries on various plants, but more especially as honey-dew which is discharged from aphides, and other Hemiptera, that live gregariously on foliage. Ants with habits of this kind may be regarded as representing the pastoral stage, and various species are able to induce aphides, and allied insects, to void honey-dew by stimulating them by means of stroking movements of the antennæ. Others shelter and protect the aphides either within, or in the neighbourhood of their nests, and Linnæus was justified in terming these creatures the dairy cattle of the ants. The pastoral habit has led to a remarkable specialization in those species known as 'honey ants', which have learned the advantages to be derived from storing honey-dew when it is available in quantity. Since no ants have acquired the faculty of even constructing cells for their larvæ, or any other types of receptacles, they have adopted the curious method of using the crops of certain worker or soldier individuals as storage chambers. Members of the colony functioning thus are termed repletes and they become so inflated in the process that they are quite unable to walk and assume the rôle of animated carboys. When hungry, the ants stroke the repletes with the

antennæ and receive from them droplets of regurgitated honey-dew. This habit has been observed in ants living in desert or other arid regions of North America, Africa and Australia.

The so-called harvesting ants which inhabit much the same terrain, where insect food is scarce or precarious to obtain, have exploited vegetable resources more directly. Certain genera belonging to the subfamily Myrmecinæ have resorted to collecting and feeding upon such plant seeds as may be available. The seeds are collected, husked and stored in special chambers or granaries and in some species the soldiers appear to function as seed-crushers, thus allowing of the softer parts of the seeds to become available for consumption by other members of the colony. These soldiers have their mandibles adapted for the purpose, and correlated changes in the size and form of the head have also taken place.

As Wheeler points out, these harvesting ants can hardly be regarded as strictly agriculturists, since they neither sow nor cultivate the plants from which they obtain the seeds. There are, however, certain ants constituting the group of the Attini, that may be more appropriately looked upon as cultivators. They are widely distributed in both North and South America and are fungus-feeders. The fungi are cultivated in special chambers of the nest and these beds, or ‘ gardens ’, are practically pure cultures of the species concerned. Alien fungi are weeded out and the beds generally tended by the workers. A fungus bed is a spongy mass of comminuted leaf-fragments, or excrement, and growing fungi produce on this substratum curious swellings termed bromatia, which serve as food for the ants and their larvæ. A queen, when about to form a new colony, ensures the continuance of the

fungal culture before finally leaving the nest. This she does by filling her infra-buccal pouch, on the floor of the mouth, with fungal hyphæ and the pellet is subsequently expelled upon the new bed which she has previously prepared. It is noteworthy that the fungi, when removed from the nest, and grown as cultures in mycological laboratories, assume very different forms, and the bromatia fail to develop under these conditions.

In Chapter III the importance and significance of trophallaxis in the social economy of wasps was referred to. The same phenomenon prevails among ants, especially in those species that have established relations with insects that exude honey-dew. Wheeler, who has paid special attention to this phase of behaviour, states that certain ant larvæ undoubtedly supply the attendant workers with saliva, while many, or all, exude a fatty secretion through the general integument of the body. In the tropical subfamily Pseudomyrminæ the desired secretion is exuded from special papillæ or larval appendages. The glandular product of these organs is eagerly imbibed by the attendant ants whose maternal care for the brood is, at least in part, directly associated with what they receive in return for their attentions. The larvæ in this subfamily are highly specialized and different from the general form they assume in other ants. The head is surrounded by the hood-like thorax, and lies far back on the ventral aspect of the body where it comes into close relation with the first abdominal segment (Fig. 13). Food supplied to the workers is deposited in a special pocket (trophothylax) situated on the last mentioned region, from which it can be slowly drawn into the mouth and consumed. Such larvæ are provided with curious appendages or exudatoria which appear to be blood-glands providing a secretory product. These appendages comprise one or

more pairs of finger-like organs, located in the ventro-lateral region of the thorax, in such a situation that they can be readily licked by the workers engaged upon feeding the larvæ.

Ants represent the most successful development of

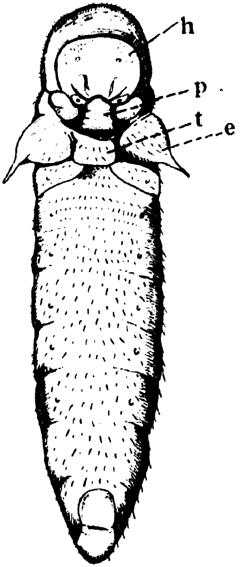


FIG. 13.—Ventral Aspect of a Larva of the Ant *Pachysima latifrons*

h, head; *p*, food pellet; *t*, trophothylax; *e*, exudatory appendage. Adapted from Wheeler.

social organization among insects. No other social group has attained their dominance among the insect fauna of the world. According to Wheeler, 6,000 different species, subspecies and varieties of ants have been described and it is probable that their numbers

will attain to 10,000 before the present century closes. Furthermore, the colonies of many of the species are exceedingly densely populated; Forel, for example, has estimated that a large mound of the European ant, *Formica pratensis*, may contain about 500,000 individuals. While this figure has been regarded as being too high by some authorities, it seems certain that such a population amounts to several hundreds of thousands. Further evidence of the dominance of these creatures is revealed in their nearly world-wide geographical range. They abound in all the continents, becoming immensely prolific in the tropics and subtropics, and are only absent from polar regions and the higher mountain tops. Their prevalent habit of adapting themselves to a subterranean life has probably contributed much to their ubiquity, and the great predominance of apterous individuals in all ant colonies is correlated with these same hypogæic conditions. Since all ants are social in behaviour, stages in the incipient development of this mode of life are no longer evident. On the other hand, it is possible to trace a very marked grading, of both habits and social organization, in passing from the lower to the higher subfamilies. The Ponerinæ appear to come nearest to the primitive phase from which the other subfamilies have presumably been derived as developments along divergent lines. They retain the sting in an effective and fully-formed condition: this organ is present also in other of the lower groups but is absent or vestigial among some of the Myrmecinæ, most of the Dolichoderinæ and in all the Formicinæ. The colonies of Ponerine ants are of small size, the workers are monomorphic and differ little in stature from the queens. In habits the species are carnivorous and live in simple ground nests. These same features are also largely shared by the Cerapachyinæ and Pseudo-

myrminæ, only in the latter subfamily the larvæ are highly specialized in the manner already explained. The Dorylinæ are likewise primitive as regards their general structure, nesting habits and carnivorous food, but, on the other hand, the workers are highly polymorphic and the queens attain relatively enormous dimensions. The Myrmecinæ are a large and heterogeneous group: the lower members are carnivorous while others are harvesters or fungus-cultivators. The two highest subfamilies are the Formicinæ and Dolichoderinæ, among which the habit of collecting honey-dew and nectar is extensively developed. The Myrmecinæ and Formicinæ, furthermore, are the only groups that have penetrated extensively beyond the tropics and become cosmopolitan in their geographical range. In the higher subfamilies it is also noteworthy that many of the most specialized genera have forsaken the ground and become arboricolous.

The complex problem of the causes of polymorphism in ants can only be very briefly referred to here. The advanced condition of caste differentiation among these insects does not appear to be explicable, except to a limited extent, on the basis of nutrition. The size differences in polymorphic series of workers appear to be largely attributable to variations in the amount of food received. When, however, we come to the more fundamental characters exhibited by the dimorphic males and females in different ants and the differences separating the winged queens from the apterous workers and soldiers, some other explanation is necessary. The available evidence leads us to conclude that, since the differences involved are so rigid and fixed, they are of an hereditary character. As Wheeler has observed, the original differences between the queens and workers may have been determined by nutritional influence in

the ancestral forms, but now the germ-plasm has become permanently modified, with the result that an heredity-basis for caste differentiation has supervened. A general elementary discussion of the subject will be found in Chapter VIII.

CHAPTER VI

THE TERMITES OR 'WHITE ANTS'

THE termites or so-called 'white ants' are, like the true ants, all social insects that live together in communities. Their whole social organization presents features of exceptional interest, not only on account of the complexity of phases that it presents, but also from the fact that, although these insects are of a remarkably primitive structure, their social life parallels in many features that of such highly evolved insects as ants. Termites number about 1,200 different species and are consequently richer in this respect than either the social bees or the social wasps. They abound throughout the tropics as well as occurring in most warm temperate lands. Only two species are common in Europe and, as a group, they are intolerant of cold.

As a rule termites are pale-coloured, soft-bodied insects with a delicate thin integument, and may be readily distinguished from ants by the absence of any constriction or 'waist' near the region where the abdomen unites with the thorax. Certain members possess two pairs of similar, elongated, membranous wings which are very readily cast off owing to the existence of a line of fracture near their bases: the vast majority of the members of a colony, however, are totally wingless. Unlike all other social insects they pass through no larval and pupal stages and their metamorphoses are often of a very slight character.

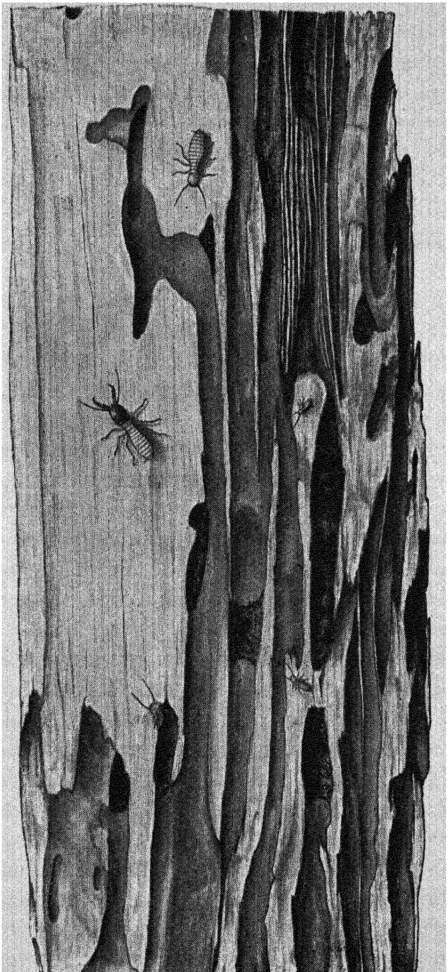


FIG. 14.—Nest of a Primitive Termite *Archotermopsis* (Himalaya) consisting of Galleries in a Log of Deodar

From the economic standpoint termites are of great importance since the chief food of a large proportion of the individuals consists of cellulose. In order to obtain this material they injure or destroy trees, shrubs, field crops and the woodwork of buildings. Owing to this propensity they entail immense losses to man, especially in the tropics. Termites occur in the soil in literally incredible numbers—almost beyond the comprehension of those who have not had experience of these creatures in the tropics. Their nests, or termitaria, are very varied in character. The more primitive species feed upon wood and they construct no true nests, but merely hollow out series of galleries in logs, decaying or declining trees, or in manufactured timber (Fig. 14). Other species burrow in the ground wherein they construct a labyrinth of tunnels, either with or without a mound nest above the surface. Among the higher termites, especially those of Australia and Africa, the termitaria are frequently gigantic structures of great durability. They are built up of earthen particles cemented together by means of saliva or with fæcal matter and, upon drying, the material assumes an almost cement-like hardness. These mounds or 'fortresses' can often only be broken asunder by laborious use of picks and they are proof against most vertebrate animals, other than those endowed with formidable claws. Some of the most remarkable of all termitaria are the lofty steeple-like structures constructed by the species *Eutermes triodiæ* in northern Australia, which are known to attain a height of 20 feet with a basal diameter measuring 12 feet (Fig. 15). In proportion to the size of the occupants they can only be compared with the skyscrapers of the city of New York. The interior of such a construction presents a maze of irregular chambers and passages, and in its deeper recesses the brood is reared and the

royal cell is located. The compass or 'meridional' termite, *Hamitermes meridionalis*, is widely distributed in Australia where its nests attain a height of 8 to 12 feet. These structures are flattened from side to side in a manner that results in the broad faces being directed

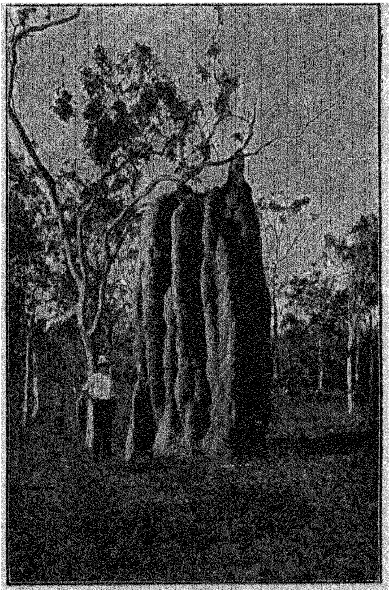


FIG. 15.—Large Termitarium of *Eutermes triodiæ*, Australia

After Hill, *Proc. Linn. Soc. N.S.W.*, *1915*.

east and west with the narrow ends north and south. It has been suggested that this peculiar and constant orientation allows of speedy desiccation and hardening by the sun during the rainy season, when they are being constructed or repaired. In some parts of the world

gigantic termitaria are congregated into 'villages' where they lend conspicuous features to the landscape. There are other termites which construct carton nests of

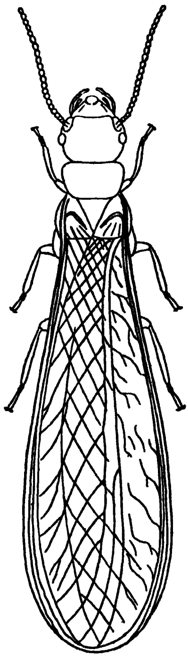


FIG. 16.—A typical Winged Termite (Macropterous form)
Coptotermes ceylonicus
After F. P. Jepson.

masticated wood, placing them up trees. Nests of this kind are ovoid or rounded, about the size of a football or larger, and comprise an outer envelope which encloses a comb-like mass of passages and chambers. There are

a number of species of termites which come above ground in search of food or water. In order to avoid exposure they construct earth-like tubes or passages which pass up the surfaces of buildings or trees, often to a great height. These covered ways are very common in parts of the tropics and within the shelter thus afforded the termites are able to move over considerable distances to and from their nests without exposure to light, and under fairly constant conditions of humidity.

Polymorphism in termites, although strikingly like that prevailing among ants, reveals certain fundamental differences. In termites the sexes are of equal importance in this respect, since each caste comprises both male and female individuals. Among ants it will be recollected that the soldiers and workers consist of females only.

In termites there are five principal castes, three being fertile reproductive castes and two are sterile castes. The reproductive castes comprise the following forms.

1. **Macropterous Forms**—These are the normal winged males and females which are usually known as the true kings and queens. They have a firm, dark integument with the eyes and brain large and the reproductive organs well developed. The large membranous wings are ultimately discarded and only their truncated bases remain (Figs. 16, 17).

2. **Brachypterous Forms**—These are sometimes designated neoteinic kings and queens. They are less pigmented, with pad-like, incipient wing-rudiments. The brain, eyes and reproductive organs are somewhat less developed than in the first form (Fig. 17).

3. **Apterous Forms**—The name ergatoid kings and queens has been applied to these forms. They have little or no pigmentation and the integument is delicate and membranous. There are no traces of wings, while

the brain, eyes and reproductive organs are less developed than in either of the preceding forms.

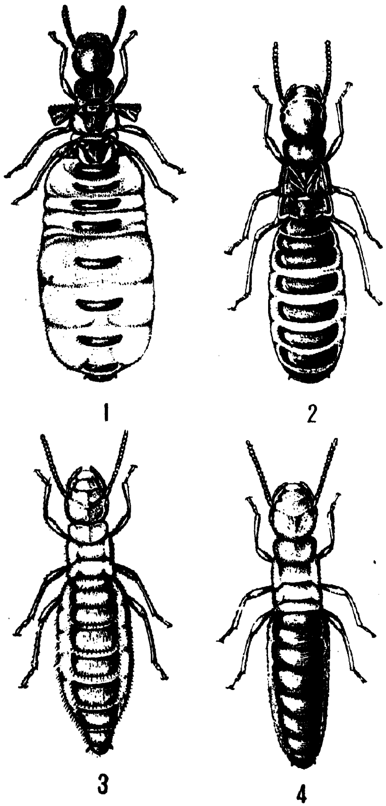
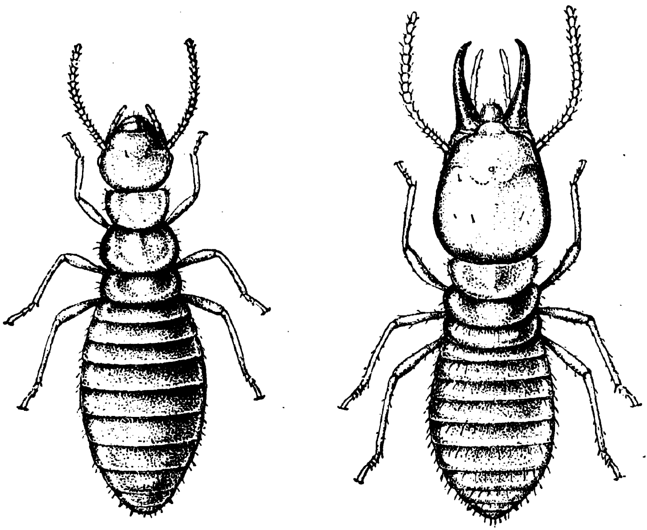


FIG 17.—1, Deälated Queen Termite, and 2, King; these are Macropterous forms which retain the Basal Stubs of the Wings. 3, Brachypterous Queen, and 4, Brachypterous King

After T. E. Snyder (*Smithsonian Misc. Coll.*, Vol. 76, No. 12).

The sterile castes are wingless and the reproductive organs are imperfectly developed and non-functional, excepting possibly in some of the most primitive species. They comprise :

4. **Workers**—In these there is little or no pigment-



1 2

FIG. 18.—*Prorhinotermes simplex* : 1, Worker ; 2, Soldier *After* H. Banks and T. E. Snyder (*U.S. Nat. Mus.*, Bull. 108).

ation, the brain is small and the eyes vestigial or absent. The head and mouth-parts are not exceptionally developed (Fig. 18). Individuals of this caste are often very like the ergatoid royal forms and, in so far as external features are concerned, their broader heads will serve

to separate them. In some species both large and small worker forms are present.

5. **Soldiers**—Large-headed and more or less pigmented individuals are termed soldiers. The mandibles are very prominent and project outwards from the head: they vary greatly in shape among different genera, often assuming bizarre forms (Fig. 18). As in

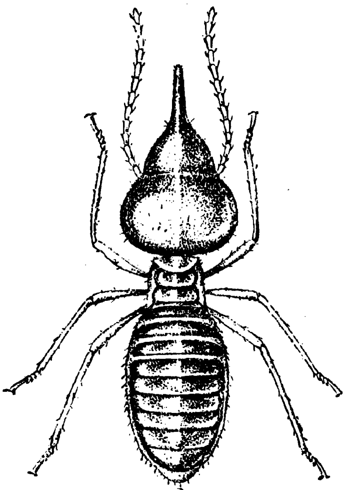


FIG. 19.—*Eutermes costaricensis*, Nasute Soldier *After* Banks and Snyder (loc. cit.).

the worker caste the brain is small and the eyes are vestigial. In certain species there may be three grades of soldiers—large, medium-sized and small. Among a few of the higher genera the usual large-jawed soldier is replaced by a type with vestigial mandibles and a retort-shaped head, which is drawn out into a rostrum bearing the opening of the large frontal gland at its

apex (Fig. 19). Individuals of this type are termed nasute soldiers and these, in their turn, may be either dimorphic or trimorphic according to their species.

At certain times of the year, generally the rainy season, the macropterous royal forms issue from the nest in large numbers and, after a brief flight, they alight on the ground and shed their wings. Vast quantities of these winged termites are devoured by birds, lizards and other animals, while the few survivors found new colonies. Each colony is established by a royal pair: together they excavate a small cavity in the ground or other situation and remain, feeding and tending their offspring, until enough workers have been reared to take over these functions. Mating occurs at irregular intervals, the king cohabiting with the queen for life. In the most primitive termites the queen undergoes little or no change of form and lays a comparatively small number of eggs from time to time. In the highest forms she attains relatively enormous dimensions owing to a process of post-metamorphic growth. The ovaries and fat-body increase greatly in size and other organs become modified in order to conform with the resulting abdominal extension. The original tergal and sternal plates become widely separated owing to the growth of the intersegmental membrane, until finally the latter forms almost the whole covering of the abdomen. As in ants, the wing-muscles degenerate and their disintegration products contribute to the nutrition of the developing parts. The king undergoes little morphological change, beyond becoming somewhat inflated as the result of a well-fed, inert life, passed in immediate proximity to the queen. These royal forms no longer partake of their original ligneous or other food but receive a prepared diet from the workers. The capacity of the queens for egg-laying exceeds that of all other

insects since they are able to produce at least a million eggs annually, and their duration of life lasts for a number of years.

It was formerly believed that if the original queen was destroyed the colony would ultimately die out, but this belief has been dispelled by the discovery of the brachypterous and apterous reproductive castes. Either one or both of the latter may be present among the offspring of the macropterous queen, and they develop into new royal forms under conditions that are at present little understood. The death of the original queen results in the colony being headed by a brachypterous or apterous form, and hence the latter are often termed substitution royal forms. It is probable that they also found separate or branch colonies, while the original queen is still alive, and they may possibly reproduce and maintain the older colonies up to strength. Colonies headed by one or other of these substitution royalties appear no longer to contain the macropterous caste. Recent observations made by Snyder and the late Miss Thompson indicate that the substitution royalties can only reproduce their own and the forms below them in the 'hierarchy'. It would, therefore, follow that the macropterous forms alone reproduce all the castes common to their species.

The workers perform almost all the communal functions. The tending of the eggs and young forms and of the royalties: the foraging for food, often at a distance from the nest: the actual nest construction, with its repair and upkeep, all devolve upon the members of this caste. In the case of lignicolous species the workers excavate the galleries and tunnels that constitute the nest. The gnawing propensity of the caste, when exercising this function, has earned for termites their unenviable reputation as destroyers of materials that serve the convenience of man. Dimorphic workers

prevail in certain of the higher termites, the caste being divisible into major and minor forms. In such cases the head and jaws, and often the general stature, are definitely larger in the major individuals. As prevails among certain ants it is, in some species, impossible to separate the workers definitely into these two types owing to the prevalence of intermediate forms.

The soldiers, in general, are concerned with the defence of the colony. They utilize their powerful jaws in seizing and ejecting intruding insects, but their efficiency in this respect is very variable. Also, the differences in size and shape of the jaws, and of the head itself, are difficult to explain on the basis of their being adaptations to specific functions. Among the higher termites nasute soldiers prevail: these, like the large-jawed forms, congregate at the surface of the nest in the event of any injury or break in its walls. They appear to be the more effective defenders of the colony and their greatly developed frontal gland, with its pungent secretion, seems to render jaws no longer necessary. This secretion, when discharged on to ants and other insect enemies, seems to disorganize their activities so thoroughly as to render them *hors de combat.*

The feeding habits of termites are both complex and remarkable. Living and dead parts of plants form their staple diet, but these insects seem to devour, almost indiscriminately, fæcal matter ejected by their fellows, together with exuviæ and even dead members of the colony. The young individuals and the royal forms are fed by the workers with regurgitated food and saliva, while it appears that all castes produce exudations or glandular products from the skin which are licked by other members of the colony. Since the queen produces the most copious exudation of this kind she is the most assiduously licked and tended by the workers. It is

evident, therefore, that trophallaxis is a notable feature in the economy of these insects as in that of wasps and ants. In fact the individuals of a colony appear to be so mutually interdependent that survival apart from their fellows is of but brief duration. Even the eggs fail to hatch unless licked and tended by the workers.

There are species of termites, as with ants, that conduct foraging expeditions, especially for procuring lichens, fragments of grass, etc., which are collected and stored within the nest for future consumption. The analogy between ant and termite behaviour is exemplified most strikingly in the case of the fungus-growing termites. Certain of the higher genera form comb-like fungus beds in special chambers of the nest. These beds are composed of a spongy dark reddish-brown 'comb' of comminuted vegetable matter and excreta. Fungi readily germinate on this substratum and produce small white spherical bodies which form the nutriment of the young individuals and the royal pair. The fungal chambers further serve as nurseries for the brood, and Bugnion states that in species observed by him in Ceylon, the juvenile termites graze on these fungus beds like miniature sheep.

A notable feature in the lives of the more primitive termites, which feed upon wood, is the presence of enormous numbers of Protozoa in their digestive canal. Formerly these organisms were looked upon as parasites, and their activities were regarded as being responsible for the production of the sterile castes. In this connexion it was maintained that the Protozoa exercised a retarding effect upon the reproductive system, ultimately resulting in a condition of castration. Recent discoveries by L. R. Cleveland, following the earlier observations of Bugnion and of Imms, show that the Protozoa are symbionts. They obtain their nutriment

by ingesting the wood particles devoured by the termites. and, in the process, the products of their digestion serve to nourish the latter insects. Cleveland has demonstrated that the termites themselves are unable to utilize ligneous matter as their food. They possess no enzyme capable of rendering its principal constituent, cellulose, in an assimilable condition. On the other hand, the Protozoa act as intermediaries in this respect, and termites deprived of these micro-organisms are no longer able to live on wood, and ultimately die of starvation. Cleveland was able to show that the Protozoa can be readily killed off, without injury to their hosts, either by incubation at 36° C. for twenty-four hours; or by starvation, or by increasing the oxygen tension of the surrounding atmosphere. Termites, thus defaunated, die within ten to twenty days if fed upon the normal woody diet, but when reinfected with Protozoa their ability to utilize wood is regained and they are able to live indefinitely. Since the Protozoa multiply and die by thousands within their hosts, their remains would appear to provide the latter with the nitrogen they require. The young termites and the royal forms contain no Protozoa and are fed upon a special assimilable diet. As the juveniles increase in age they commence to devour the fæcal matter ejected by the older forms, and in this way they soon become infected with the necessary micro-organisms and are able, in their turn, to resort to a wood-feeding habit. The higher termites feed on fungi and material other than wood and, in these cases, the symbiotic Protozoa are wanting.

Termites are second only to ants in point of numerical dominance of their species. It is tolerably certain, however, that the individual population of a large termitarium is little, if at all, less numerous than that of

a well-established ant stronghold. The security afforded by subterranean life has played an even more predominating part in the evolution of termites than of ants. Termites are wedded more exclusively to the soil; within the shelter of their mounds and subterranean labyrinths they have 'dug themselves in' so securely that they are less prone to come out into the open and incur the risks involved. Their adaptations, whether expressed by degeneration or other ways, to the hypogæic life are more complete. Within the seclusion of these habitations, the queens reproduce and the life of the colony goes on. It is only in certain species that sorties are necessitated and the outside world scoured for food. As with ants, the general absence of wings is a predominating feature, while in all except the royal forms, the eyes have mostly become either vestigial or lost altogether. The macropterous royal forms alone are aerial and yet, as in ants, they soon shed their wings once the transitory function of these organs has been fulfilled. The similar development of sterile castes along the two parallel lines of polymorphic workers and polymorphic soldiers is, in itself, a remarkable fact when we reflect that in one case it has come about in a group consisting of little more than lowly colonial cockroaches, and in the other among the highly evolved derivatives of the wasps. The parallelism does not stop here: the two groups have acquired the similar habit of fungus cultivation along almost identical lines: trophallaxis prevails in both: there are similar mating flights of the royal forms: there are many likenesses in colony formation and nest-construction: and, as will be seen in Chapter VII, the relations with inquilines and symbionts among other insects is closely approximated in these two groups. Wheeler also has commented upon the duplication of these phenomena in

groups so wide asunder that they are placed at opposite poles in the scheme of insect classification. He remarks on the similarity of human cultures and linguistic peculiarities among widely separated peoples. While some anthropologists attribute such similarities to community of origin, others ascribe to them an independent development. 'When,' he adds, 'we reflect that ants and termites have been able, through slow physiological and instinctive processes, independently to evolve such strikingly analogous peculiarities . . ., we can scarcely doubt that different human communities, belonging to the same species and endowed with the same intelligence, may frequently have hit upon the same inventions.'

CHAPTER VII

SOCIAL PARASITISM AND OTHER RELATIONSHIPS

I. Social Parasitism[1]

PARASITISM by one species of insect on another is a common feature well known to the entomologist. There are vast groups of insect species, such as the parasitic Hymenoptera and the Tachinidæ among Diptera, whose individuals develop at the expense of the tissues of other insects which serve as their hosts. Among social insects we are concerned with a somewhat different kind of parasitism, for the reason that the members of one colony live at the expense of those of another colony of a different species. It might well be termed family parasitism in the sense that the individuals of a single colony of a social insect represent a unit or family. The members of a colony, therefore, are not individual parasites of individual hosts. Social parasites exhibit very diverse relationships with their host species, varying both in character and intimacy. Their type of behaviour occurs in all the main groups of social insects, but is most pronounced and has been most thoroughly investigated in ants. It prevails among closely related species and genera, and from this fact we are led to conclude that such parasites find the most favourable

[1] Social parasites are often termed inquilines or 'cuckoo-parasites'.

conditions among hosts whose habits and economy are not markedly different from their own.

Among bees there are many examples of parasitism among the solitary species, while the best known and clearest case of social parasitism is afforded by the genus *Psithyrus* which, along with *Bombus*, forms the family Bombidæ. All the members of the first mentioned genus share both food and nest with species of *Bombus*. Generally the parasitic species is closely associated with a particular host species and bears a striking resemblance in size and colouring to the latter. Thus, in the British fauna, *Psithyrus rupestris* closely resembles *Bombus lapidarius* and *P. vestalis* likewise simulates *B. lucorum*. According to Sladen, the overwintered queen of a *Psithyrus* enters a young nest of *Bombus* in spring, after the earlier workers have appeared. Sooner or later she stings the host queen to death, thereby eliminating the production of further workers, with the result that the existing members of this caste rear the Psithyrine offspring. This change in the economy of the host species proceeds amicably and the parasitic brood is reared with the same fidelity as if it were the offspring of the *Bombus* itself. In nests affected by this kind of parasitism the host population becomes naturally greatly reduced, and the parasite, from the nature of its life, produces only ordinary males and females, its worker caste being wanting. Individual Psithyri differ from the corresponding males and females of their hosts in their more resistant and more shiny cuticle which, in so far as the abdomen is concerned, is less densely clothed with hair. Since the females do no foraging on their own account, they have lost the polliniferous apparatus, and the outer surface of the hind tibia is convex and uniformly hairy. In *Bombus*, on the other hand, it is more or less concave, bare and glistening, and marginally

clothed with long hairs to retain the pollen as it is collected. Sladen stresses the close resemblance in other characters between *Bombus* and *Psithyrus* which extends to nearly all details of structure, and he states that it is impossible to avoid the conclusion that the parasite genus has been derived from its host. This dictum is in accordance with the views of Wheeler who gives additional reasons for believing that the parasitic habit has arisen, in all cases among social insects, among members of the same species. In times of scarcity of food they have found it advantageous to plunder the nests of their neighbours : also, the urgency of the egg-laying reflex would reinforce this robbing propensity in tending to establish the parasitic habit. This conclusion is further supported in the case of the few known parasites among wasps. Thus, in the British species *Vespa austriaca*, and in the North American species *V. arctica*, the worker caste is likewise unknown. In the case of *V. austriaca* the host is the common wasp *V. rufa*, in whose nests it is reared. G. H. Carpenter and D. R. Pack-Beresford have shown that these two wasps are so closely related in all details of their structure and coloration, that their males and females might well be regarded as merely slightly different forms of a single species, were not the parasitic habit disclosed among the Bombidæ. The North American *Vespa arctica* enters the nest of *V. diabolica*, to which it is likewise closely related, where the female lays her eggs and her larvæ are reared along with those of the legitimate owners of the nest.

The relations between ant communities of different species are of a varied character. In some cases two species of these insects may occupy a compound nest, and live on amicable terms, although their respective broods may be kept apart. Relations of this kind are

of the nature of social symbiosis rather than of parasitism: in other cases different ant colonies, even of the same species, may live in close proximity to one another, but on more or less antagonistic terms. One species may succeed in obtaining at least a portion of its sustenance by waylaying the workers of the other species, when the latter are returning to the nest laden with provender. Aggressive ants, with this kind of behaviour, form their nests in proximity to those of the species they intend to plunder. In a rudimentary phase of this kind we see the beginnings of social parasitism. There are other ants, of predaceous instincts, that raid the nests of more pacific species and carry off their brood for food, sometimes killing the adults. Behaviour of this kind may perhaps be best termed social predatism. The peculiar habit known as dulosis or slavery, occurs among certain ants and is well exemplified in the European *Formica sanguinea*. The workers of this species are parasitic upon the allied *Formica fusca*, and other ants, in the sense that they carry off to their own nests pupæ from which workers will subsequently develop. Such workers live as slaves in the abodes of their captors, but the latter are not entirely dependent upon them since they are capable of forming independent, slaveless nests on their own account. Obligatory slave-makers, or the so-called 'amazons', are represented in Europe by the species *Polyergus rufescens*, which is dependent upon its slaves in whose nests its young queens establish their own brood. The young *Polyergus* queen enters a weak colony of *Formica fusca*, and secures adoption, after killing the rightful queen with her sharp mandibles. She then produces progeny which, when mature, will make actual slave-raids into other *fusca* colonies. The larvæ and pupæ obtained from the latter give rise to workers that do all the necessary nest-

construction, feed the *Polyergus* and bring up her brood but take no part in the slave-raiding itself. It will be noted, therefore, that the *Polyergus* is parasitic upon the nest of another ant species whose workers perform all the necessary communistic duties. The *Polyergus* workers, in their turn, are solely concerned in maintaining the slave population at the requisite level. In addition to these slave-making instincts, there are other ants defined by Wheeler as temporary or permanent social parasites. In the first-mentioned category is the species *Bothriomyrmex decapitans* of Tunis, whose economy has been to some extent unravelled by F. Santschi. The newly fecundated female of this ant wanders about in search of a nest of *Tapinoma nigerrimum*, and when in its proximity workers of the latter species seize or 'arrest' her and drag her inside. If the *Tapinoma* ants prove unduly hostile she takes refuge on the brood or on the back of the larger *Tapinoma* queen. In such situations her own characteristic odour becomes masked by that of the host colony. While on the back of the host queen she may employ herself in decapitating her, and she gradually acquires a sufficiency of the nest odour to become accepted as the ruling queen. The *Tapinoma* workers tend her brood and, as they gradually die off with age, the whole colony ultimately becomes a thriving 'pure culture' of *Bothriomyrmex*. In the permanent social parasites the worker caste has become entirely eliminated, as in *Psithyrus* among parasitic bees. This phase of relationship is well exhibited in the European ant, *Anergates atratulus*. This species lives entirely at the expense of *Tetramorium cæspitum*, the queen entering the nest of the latter in order to take up permanent abode there. Although small, and provided with wings at the time of her entry into the host nest, she soon casts these appendages and

gradually develops into an inert organism with an enormously enlarged abdomen. The *Tetramorium* workers assassinate their own queen and tend the *Anergates* brood, which comprises only males and females. The resulting colony, therefore, is of a mixed character, and terminates with the death of the last of the host workers. The male *Anergates* exhibit remarkable degeneration consequent upon their parasitic life, and are wingless pupa-like creatures incapable of leaving the nest. They have to mate, of necessity, with the females derived from the same brood as themselves, and their fecundated partners then leave the nest in search for new *Tetramorium* colonies.

Among termites it is by no means uncommon to find two or more species nesting in a common series of galleries : as many as eight different species are recorded by Holmgren as living within the confines of one termitarium. There is no evidence of parasitism in instances of this kind : most likely, little more than an amicable association is involved and without any real symbiotic relationships. Instances of plundering have been noted among these insects, and particular mention may be made of a South American species of *Microtermes*, which is recorded by Silvestri as ravaging the stored food supplies of a member of the genus *Eutermes*. There are again termites which are only known to occur in the mounds of other species : this association is so constant as to suggest that the occurrence of parasitism is not beyond the bounds of possibility. In the unique genus *Anoplotermes* there is no soldier caste and, since the species largely frequent nests of other termites which have well-developed soldiers, further enquiry may reveal the occurrence of some form of parasitic relationship.

Viewing parasitism among social insects, as a whole, one is impressed by its comparative rarity. The para-

sitic species themselves are, with few exceptions, far from common, and their individual populations are very low in numbers. Their hosts, however, are always common and widespread with numerically abundant colonies. The occurrence of parasitism seems to be too infrequent to assail their predominance, while at the same time the parasitic species themselves appear to have benefited comparatively little by the experiment which appears, on the other hand, to have contributed to their decline.

II. Relations with Other Insects, etc.

The ecological conditions associated with insect life in communities have been exploited by a heterogeneous assemblage of other creatures. This alien population comprises not only insects of almost all orders, but also a diverse collection of Arachnida, land Isopoda and Myriapoda. The nest of a social species provides not only food and shelter, but also more equable conditions of life than prevail in the outside world, to all such foreign invaders as are able to establish themselves within it. Possibly dense populations of individual insects in society tend to make its component members tolerant of alien residents: or, perhaps, in some cases frequent intrusion of the latter has been productive of indifference to their presence; in other cases the aliens themselves have agreeable offerings to their hosts so that their presence soon becomes accepted. Whatever the underlying causes may be, it is a general rule that the more populous the social community becomes the larger is the alien population it seems destined to support. At least 2,000 species of these inhabitants (myrmecophiles) are known to live in association with ants: about 700 species (termitophiles) occur along with termites, while both social wasps and social bees have their own specific

forms. The conditions of life in termites' nests have induced the establishment of a termitophilous fauna closely analogous to that composed of myrmecophiles: the relationships of aliens and hosts are very closely paralleled in the two cases, and afford yet another example of similarity of ecology and behaviour in the two main streams of social life among insects. The eminent Jesuit, E. Wasmann, has devoted life-long study to such arthropod invaders of the social medium, and has classified them into different categories in accordance with their specific host relationships.

There are, for example, *synechthrans*, or hostile persecuted species, that are treated with marked antagonism by their hosts. They are agile creatures that are able to elude the senses of the normal occupants of the nest which they seek to enter. Various genera of Staphylinid beetles, so frequent in ants' nests, come under this category, and they mostly prey upon their hosts or the brood. The *synœketes* are indifferently tolerated species that live along with their hosts without arousing antagonism on the part of the latter. They form the largest group of alien intruders in the abodes of ants and termites and comprise Coleoptera, Lepidoptera, Diptera, Hemiptera, Orthoptera, Apterygota, Acarina, etc. In habits they seem to be mainly scavengers feeding upon nest refuse of various kinds. The *symphiles* or true guests are all highly adapted to their mode of life. Such species are amicably treated, licked, fed and even reared by their hosts. Those inhabiting ants' nests comprise many Coleoptera which, although representing diverse families, exhibit a remarkable adaptive convergence in their structural characters. This is shown in their general similarity of colouring, their antennal characters, mouth-parts and gland development. These symphiles are assiduously licked by the ants which are attracted

to them by the aromatic secretions provided. Such secretions exude through special cuticular pores, and especially among localized patches of very characteristic yellow or red hairs, which aid in the diffusion of these glandular products. In their turn, the guests may be fed by the ants and their larvæ may be tended and fed, while those of the symphiline beetle *Lomechusa* are even allowed to prey upon the eggs and brood of their hosts. The symphile inhabitants of termite nests include some of the most bizarre forms of insect life. Many are characterized by physogastry, or excessive enlargement of the abdomen, which is often due to a great increase in the fatty tissues or abnormal growth of the alimentary canal or gonads. In certain species the body may be furnished with glandular outgrowths or exudatoria, which assume extraordinary shapes and forms. Such creatures are either wingless, or have their wings much reduced or hypertrophied, or even converted into exudatoria. All these curious developments are correlated with the production of exudates that are eagerly licked up by their hosts, and the guests in return are either fed with regurgitated food or allowed to prey upon the brood of their attendants. Several of these extraordinary symphiles are shown in Fig. 20. They include Staphylinid beetles, Psychodid and other flies or their larvæ. In a fourth category are the true *parasites*, which live either externally or internally in relation to their hosts or the brood. To the foregoing have to be added the so-called *trophobionts* that occur in relation with ants. These creatures include aphides, coccids and other Hemiptera, etc., which exude honey-dew, and larvæ of the Lycænidæ, or blue butterflies, which produce attractive secretions. Such organisms are regularly protected and tended by the ants in virtue of the products they yield. For the most part they live outside the nests, but there are

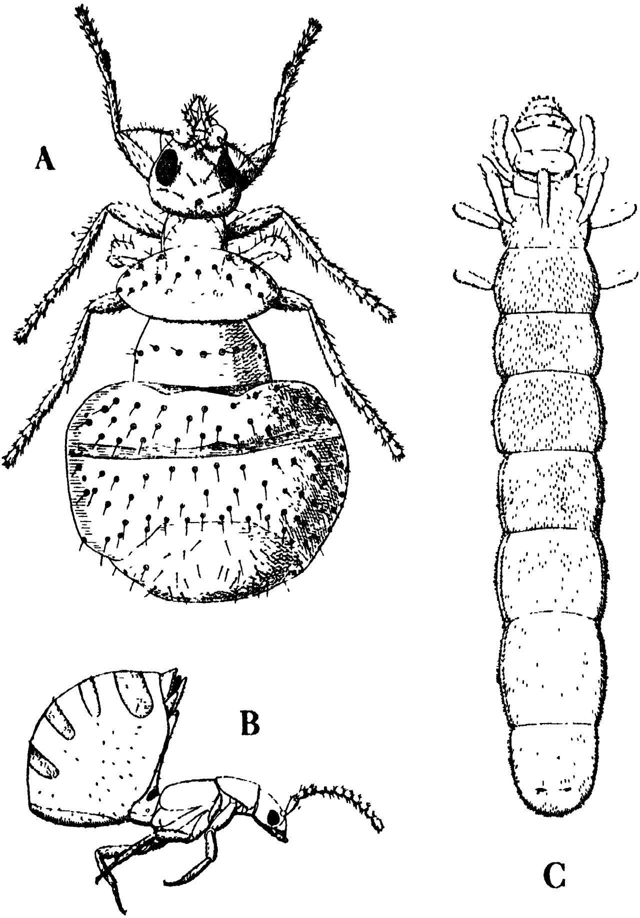


FIG. 20.—Termitophiles

A, Phorid fly, *Ptochomyia afra*, from nest of *Ancistrotermes*, West Africa. *B*, Staphylinid beetle, *Termitoptochus indicus*, from nest of *Eutermes*, Singapore. *C*, Larva of Anthomyiid fly (?), *Prosthetosoma guineense*, from nest of *Procubitermes*, West Africa. Adapted from F. Silvestri.

species that are found either permanently, or temporarily, located within.

Of all the abundant fauna of the kind just mentioned the most significant of its components are the symphiles. It has been seen that it is in connexion with these types that both ants and termites have established trophallactic relations. It would seem that the very same instincts that bind together parents and progeny have been invoked in the host-symphile relationship. While many of the alien inhabitants that exhibit this kind of behaviour are true symphiles, in that their presence leads to no deleterious consequences for their hosts, there are others which merit the term ‘ pseudo-symphiles ’. These latter merely enter into the relationship for the purpose of taking a nefarious advantage of their hosts in various ways. For most of their lives they are predators or parasites that nourish themselves on the host's brood. Thus, the parasitic Hymenopteran *Tetramopria* has tufted golden trichomes that are eagerly licked by ants. This very temporary symphily is but the prelude to parasitism, since the presence of the *Tetramopria* is primarily for the purpose of laying eggs that will hatch into endoparasites of the ant larvæ. It will be seen, therefore, that the trophallactic instinct governs social behaviour so rigidly that its ultimate consequences may sometimes appear to be anti-social in effect.

CHAPTER VIII

CASTE PRODUCTION

THE perennial enigma that has exercised the minds of so many biologists is how to account for the production of the different castes that prevail among social insects. The existence of this specialization of individuals forms the basis of the social organism. The most highly evolved, the most populous and most successful of social insects exhibit the highest phases of caste differentiation. Two separate problems present themselves in this connexion. First, how to account for caste production at all: and secondly, once it has asserted itself, how do castes, which in themselves are mostly sterile, secure representation in the germ-plasm of the species in each successive generation. The two problems are closely interlocked and the various theories that have been advanced as explanations may be grouped under (*a*) those which invoke extrinsic causes and (*b*) those which invoke intrinsic causes. The essential features connected with these respective viewpoints form the subject of this chapter.

I. THEORIES OF EXTRINSIC CAUSES

The views of those who uphold the influence of extrinsic causes, in relation to caste production, all centre round the subject of nutrition. The influence of food upon relative size among different individuals of any one species of insect is beyond dispute, and it

evidences itself over and over again in the development of the social species. When we come to caste-differences, something more than mere size is involved. In the case of wasps and bumble bees it has been already shown that the external differences between workers and queens are trivial. Sometimes, dissection alone will disclose the two types of individuals in the rudimentary character of the reproductive organs in the workers. Intermediate grades between the two forms also sometimes occur. In these relatively simple cases quantitative feeding may account for all the caste differentiation that is evident.

The prevailing opinion with respect to the hive bee is that differences in diet control the somatic differences between the queen and the workers. Taken as an isolated case the facts seem to justify this conclusion well. The German apiarist, H. von Buttel-Reepen, and others before him, found that an egg, or a young larva, when transferred from a worker cell to a queen cell develops into a queen. The influence of the special diet of 'royal jelly' is the accepted cause of the transformation. By varying the age of the larva, when the transfer takes place, it has been possible to obtain a more or less graded series of females. Should the transfer take place when the larva has passed its fourth day of age the resulting queens are smaller than normal, and decidedly more like workers. From what has been said in a previous chapter, it appears as if the normal worker diet is of a nature that inhibits the full development of the reproductive system, and results in 'nutricial' castration. Correlated with this feature certain structural differences in the secondary characters supervene.

When we turn to the related bees belonging to the genus *Melipona* we find that, unlike the hive bee, both queen and worker larvæ are nourished on the same kind

of food in an identical manner. The cells are of the same size, they are mass-provisioned with honey and pollen, and an egg is deposited in each. The cells are then sealed up and, notwithstanding this apparently identical treatment, sharply differentiated queens and workers result. Upon emergence, however, the queens have their ovaries poorly developed with the egg-cells very small, full maturity taking place later on. In the closely related genus *Trigona*, the queens are reared, as in the hive bee, in markedly larger cells. They receive larger amounts of food than is given to the workers, with the result that when they issue forth their ovaries are well formed and full of mature eggs. As Wheeler has pointed out, these facts would seem to indicate that the large size of the queen cell in this case, and consequently its greater storage capacity for food, are primarily for the purpose of accelerating the growth of the ovaries of the queen. If this be so, then such structural differences, that exist between the queens and workers, would presumably be predetermined in the eggs.

Among ants there is no very exact evidence tending to prove a direct dependence of caste differentiation upon variants of nutrition. The food in different groups of these insects is so unlike that of other of the groups that, if one kind of diet was responsible for caste production in one case, we should have to postulate that a different diet produced the same result in another species. It is possible that the queens are produced as the result of a different dietary regime from that given to the workers. The distinguished myrmecologist, C. Emery, concluded that they were only produced from larvæ that received regurgitated food, and that those which developed into workers received either animal or vegetable food in a raw, unprepared state. It is extremely

difficult to ascertain whether food differences of this kind exercise any influence in the matter, or to prove that a specific kind of feeding is absolutely confined to a particular type of individual that may result. While there may be truth in Emery's views, we are faced, in ants, with the problem of accounting for winged and wingless queens in one species, similarly dimorphic males in another, while either or both species may exhibit the very marked differentiation among its sterile castes that expresses itself in the workers and soldiers. The very rigidity and constancy of the characters differentiating members of the two latter castes, and the very evident structurally adaptive features that are both present in different species, are hard to explain upon any nutritional hypothesis. The whole problem is further complicated by the fact that the most specialized castes are normally sterile and are, therefore, incapable of transmitting their peculiarities to future generations.

Before proceeding further with the subject of caste differentiation in ants it is desirable to outline the problem with reference to termites. A number of authorities have maintained that nutrition and methods of feeding are of paramount importance in the matter. They claim that when the young termites issue from the egg they are all morphologically alike, but that very soon differentiation into small-headed and large-headed forms asserts itself. The small-headed individuals result from being fed upon a highly nutritious diet largely consisting of saliva. Acceleration of the development of the reproductive organs results so that fertile males and females are ultimately produced. The large-headed individuals are inhibited both as regards their somatic and sexual characters, owing to being fed upon a relatively poor diet of wood or other cellulose material with little or no admixture of saliva. As the result of

this kind of diet, only sterile castes are produced, but it is difficult on this basis to explain their further structural and adaptive differentiation into soldier and worker forms. Holmgren seeks to explain the whole problem on the basis of trophallaxis. According to him, certain of the very young termites receive rather more nutritious food than their fellows and produce, in consequence, a more profuse cutaneous exudation. Such individuals are more assiduously licked and tended by the workers than any others, with the result that they finally develop into sexual forms. Individuals less lavishly nourished produce less of the exudation so favoured by their worker attendants, and they finally produce sterile soldiers and workers. There are, again, other authorities who believe that differential feeding only exercises an indirect influence in that it provides the stimulus which alone allows of potentialities, already defined in the egg, to attain their full expression.

It needs to be remembered that, in experiments conducted with ants and termites, isolation of individual members of a colony, which would be the ideal method of solving their complex problems, is impracticable. Such individuals fail to develop, or die speedily, when removed from the proximity of their fellows. While the existence of such experimental difficulties, and also those attending observations on communities, demand particularly critical examination of any nutritional hypothesis that may be put forward, the influence of diet cannot be entirely dismissed as a factor in the problem of caste production. All that can be said is that the evidence in its favour is insufficient to enable us to accept it as the whole explanation of the incidence of the remarkable series of polymorphic individuals among both ants and termites.

II. Theories of Intrinsic Causes

Difficulties in accepting the nutrition hypothesis have led certain modern biologists to explain caste production on the basis that it is predetermined in the egg. Although it is admitted that differences in nutrition may account for the prevalence of graded sizes of individuals of a caste, it is contended that they do not explain the incidence of the actual caste itself. Exponents of theories of intrinsic causes have mainly concerned themselves with the phenomena of caste production among termites, nevertheless the same arguments appear to be applicable to a considerable extent to ants also. In the first instance they have sought to prove that young termite individuals, upon emergence from the egg, are already morphologically differentiated among themselves. While such individuals may be all alike externally, it is claimed that internally they are different, and are divisible into two types. These are distinguished by differences in the relative size of the brain, in relation to that of the head, of the compound eyes and of the sexual organs. Their further differentiation into small-headed and large-headed forms soon follows. The small-headed individuals, with relatively large brains and better formed eye rudiments and sexual organs, develop into the reproductive castes. The large-headed individuals with brains, eye rudiments and sexual organs, of relatively smaller dimensions, grow into the sterile castes. Very shortly, each of these two types show further development into the several reproductive castes on the one hand, and into workers and soldiers on the other. All such differences, it is claimed, are due to blastogenic or intrinsic factors only. The existence of individuals, predetermined in this way, has naturally been challenged by exponents of the nutrition hypothesis.

On the whole, however, they have not been able to advance very convincing evidence in support of their contentions. As the basis of the nutritional hypothesis, we have to believe that the profound changes in the morphology of the head, mandibles, labium, tentorium, eyes and nervous system, together with the loss of wings, which have led to the development of the termite soldier and distinguish this caste from other individuals of a species, have been produced as the result of dietary regulation. When we come to consider the genus *Rhinotermes*, even more complex difficulties present themselves. Here, it is necessary to account for the production of two entirely different types of soldiers, within the limits of a single species. *Rhinotermes* is unique in possessing not only soldiers of the usual mandibulate kind, but also highly specialized nasute individuals which exhibit entirely different morphological features (*vide* also p. 75). One of the most often-quoted examples of nutritional influence is seen in the inhibition of growth in the sexual organs. In termites there is reason to believe that the morphological characters of the soldier may have been acquired before such inhibition set in. In order to make this clear, we must examine the soldiers of the primitive Himalayan termite *Archotermopsis*. Here we find that the members of this caste betray no sign of reduction in the sexual organs. In fact, the evidence suggests that they are fertile. Furthermore, in the allied genus *Termopsis*, much the same condition prevails, and the soldiers occasionally mate with members of a reproductive caste and produce fertile eggs. In the light of these observations there is no certain proof that the soldier, or the worker, castes have resulted from the sterilizing influence of inferior nutrition.

We are, therefore, led to conclude that a more probable

explanation is that polymorphism, of the type found in ants and termites, is predetermined in the germ-plasm. It is possible that the first step in its evolution among termites was the occurrence of dimorphic males and females, one form tending to winglessness and increased head-development, the other remaining normal. Later on, the wingless form became further differentiated and ultimately lost its fertility. Correlated with this loss, degeneration of the sexual organs resulted until, in the highest forms, they are so small as to be hard to detect. Once certain castes have become sterile their persistence, on the above theory, will not necessarily cease. Assuming that the reproductive castes are heterozygous, the sterile forms will arise in each successive generation by the recombination of the respective genes involved.

A full technical discussion of these problems is out of place here. Having sketched out their general nature, and outlined current theories, we have to leave the reader to consult the special literature on the subject should it be desired to pursue the matter further.

CHAPTER IX

GENERALITIES AND CONCLUSIONS

(1)—THE behaviour of social insects differs from that of solitary species in that it has attained a higher phase of development and is, consequently, more complex in its character. Such creatures are, *par excellence*, the exponents of all that can be achieved by instinctive acts. A close correlation exists between instincts and anatomical structure—the more highly elaborated does the latter become, the greater is the play afforded for the expression of instincts. It is tolerably clear that the range of such phases of behaviour, displayed among social insects, is linked up with the diversity of 'structure that is exhibited in different species and in different castes. The close mutual association of large numbers of individuals of a species tends to promote actions undisplayed in the lives of solitary insects. Also, many social insects are relatively long-lived which allows of their negotiating a wider range of eventualities than falls to the lot of the solitary insect. Further, many actions are subjected to constant repetition in a lengthened life and, in this manner, precision is gained. Actions, that originally arose out of plastic behaviour, thus become so stereotyped as to be no longer anything more than ordinary instincts.

Two very marked features in the behaviour of social insects are its plasticity or modifiability, and the preva-

lence of what may be termed organic memory, or the capacity for retaining in the brain cells 'engrams' of experience. In this connexion an observation by H. von Buttel-Reepen, with respect to the visits of hive bees to buckwheat, may be quoted. In the neighbourhood of this crop the bees are very active from the early morning up to about 10 a.m.: for much of the remainder of the day they are resting, but commence their activities again during the same period the following day. The buckwheat, it may be added, only secretes nectar in the first part of the morning and, owing to this fact, the bees soon learn to avoid making useless mid-day flights. Notwithstanding the field of brilliant flowers, and a pervading perfume, he noted very few bees in the field once the secretion of nectar lapsed into abeyance. In this observation both adaptability to meet circumstances and organic memory are involved.

The literature on social insects contains records of many observations that indicate the existence of some sort of associative memory, which retains visual or olfactory impressions, but with regard to the actual nature of the psychic processes involved little can be said. The foraging and homing instincts of ants appear to have developed, in many cases, out of what Forel has termed the contact-odour sense. By means of their antennal sensory organs they are enabled to follow the odoriferous trails laid down by themselves, or by other members of the colony. Ants, in their developmental stages, become inured to the stimuli of the odours of other members of the nest, and responses to such odours are of the nature of conditioned reflexes, to use Pavlov's expression. Recognition of friends and foes, and of many myrmecophiles, is achieved by the same means and, in such examples, Bethe has contended that simple reflex behaviour alone is involved. While reflexes un-

doubtedly form the basis of such actions, they will not explain the fact that, once an ant has discovered a suitable location for a new nest, it then returns to the old one, and induces the rest of the colony to migrate to the fresh site. Neither will it explain why some ants, when out foraging, return by the same tortuous track they used in the outward journey, while others return by a direct route.

Among species of *Formica*, the contact-odour sense appears to play little or no part in connexion with the homing instinct. Vision, on the other hand, seems to take its place, and if the eyes of such ants be varnished over they are no longer able to find their way. Topographical memory of visual impressions appears to be the primary factor which guides not only certain ants, but also bees and wasps, while engaged upon journeys at a distance from the nest. Experiments by Rau have shown that bumble bees, when transferred beyond the radius of the territory that has already become familiar to them, either make a tardy return to the nest or become lost altogether.

Under certain circumstances, especially when confined in observation nests, ants no longer betray their usual behaviour: they may even exhibit evident signs of what in the higher animals would be termed domestication. They adapt themselves to entirely new circumstances without the prior guidance of any hereditary experience of similar adjustments. Many other examples of plastic behaviour in ants, and different social insects, might be quoted. They all point to the conclusion that such creatures not only react to new circumstances by new actions, but they also retain memory of prior sensations, associate these with the new and, in this way, meet fresh eventualities. As Fabre has said, pure instinct alone would leave the insect helpless in the

perpetual conflict of circumstances. Notwithstanding the predominance of highly complex instinctive acts among social insects, these do not provide the whole explanation of their behaviour. It would appear that we have to recognize the existence of some higher domain of psychic power in a rudimentary phase and, from analogy with our own mental processes, the only word which can be appropriately applied is intelligence.

(2)—The following of their unbridled reproductive instincts, by all the inhabitants of an insect society, would result in chaos and disorganization, unless means of alleviating such a state of affairs were developed. Not only would the population speedily outrun the food supply and accommodation, but the colony would also disintegrate into small and relatively defenceless coteries of individuals. It has been shown in an earlier chapter that, in the more primitive wasps, all the members of a colony may be capable of reproduction. Their fecundity, however, is low and the dangers of overpopulation are counteracted by the frequent emission of swarms.

The higher social insects, so abundant in individuals, are more ominously faced with this same tendency to overpopulation. The eventuality has been overcome, however, by a rigid system of repressing reproduction. It has so come about that this function is confined either to a single female (or queen) or to a small number of such individuals, of enhanced fecundity, and suppressed in all other members of her sex. Wherever this monogynous condition prevails it appears, on the face of it, to be highly precarious from the standpoint of racial survival. Such a predicament may be circumvented, or provided for, in several ways. The queen passes nearly the whole period of her life within the recesses of the nest and is, in consequence, protected from most dangers and vicissitudes that would otherwise affect her survival.

Among bees and wasps the arming of a numerous retinue with effective stings, together with their instinctive readiness to take combined action should the existence of the colony be menaced, affords a generous means of protection. Among ants, hordes of active individuals ever ready to bite, and often to sting also, have a like significance. Many species of termites are secure in their earthen fortresses and the enemies they dread most are ants. In some of the highest termites, and often in the most densely populated colonies, the existence of means of chemical warfare, on the part of the nasute individuals of the soldier caste, provides a form of defence which few ants can satisfactorily circumvent. Actual provision against consequences following the loss of the parent female is ensured in all social insects by her replacement in one or other of the several ways that have been already described.

(3)—The specialized deployment of the reproductive instinct in an insect society is, as we have seen, intimately linked up with the incidence of sterile castes. The members of such castes constitute almost the whole of the population of such a society. They, themselves, have become differentiated both structurally and instinctively in various ways for the purpose of maintaining the remaining essentials of social life, viz., food, accommodation and defence. In the hive bee, these and other functions are performed successively by each individual during different phases of its life. When we consider the densely populated colonies of ants and termites it would appear that some more advanced method of division of labour has become essential. We consequently find structural and instinctive differentiation into an essentially industrial or worker caste, and a caste composed of other individuals, or soldiers, whose functions are chiefly concerned with matters of defence and

offence. This caste differentiation is so ancient and so firmly established that all the members, whether they be workers or soldiers, are hereditarily endowed with their required attributes as soon as they are fully mature. They afford clear examples of hereditary occupations, and the behaviour of the individuals which follow those occupations has become directed into expressions of unceasing selfless industry for the common weal. Social insects have, therefore, achieved remarkable control of an essentially biological type. In further illustration of this same feature, it will be recalled that ants have developed sufficient control over some forms of insect life to have succeeded in domesticating them. The so-called trophobionts are, in effect, domesticated animals that are tended and sheltered by the ants on account of the acceptable products, in the form of honey-dew or of glandular exudates, which they yield.

The control exercised by social insects over the inanimate world is not less noteworthy. Since they have not acquired the use of tools, they have to rely upon their natural equipment of mandibles, legs, stomachs and sundry glandular secretions for their achievements in comb-building and other features or architectural design. Whether we select as an example the delicate and elaborate nests of the higher wasps, with their suspended tiers of storied cells and surrounding insulating envelopes; or the durable towering buildings of termites, with their labyrinths of internal accommodation, both exemplify the extraordinary control social insects have achieved over the use of materials.

(4)—It is a remarkable fact that among insects social habits should have arisen independently in so many groups of solitary insects. The various examples of this type of behaviour represent, as we have seen, very different stages in the evolution of the social system.

Among the simplest cases only mere rudiments of social behaviour betray themselves, while at the opposite extreme are highly specialized organizations involving immensely populous communities presenting many similarities or analogies to human society. An insect society has often been compared to a kind of super-organism whose members, although they now function as parts, were derived from ancestors that functioned as wholes. The differentiation into castes, both as regards structure and function, have been compared with the division of function among different organs of the animal body. A single individual is incapable of any lengthy survival apart from its fellow-members of an insect community, almost like the separate organs of an animal body are incapable of independent existence. The workers and soldiers may be looked upon as the body of the super-organism, while the fertile individuals represent its gonads and germ-cells.

A rather different, and perhaps more strictly analogous, form of comparison might be made with a highly civilized human community. Here we find that specialization of caste functions likewise results in the dependence of the life of the individual upon the activities of his fellows. In isolation the highly civilized human being soon discovers that even bare subsistence is an impossibility. If he is to live at all, some sort of relationship with his fellow creatures is necessary, even if he has to resort to thieving, and thereby becomes dependent upon the community in the guise of a predator or parasite. Over-population, in so far as it affects human society, may obtain partial relief by emigration (which is, in effect, swarming) to lands affording better opportunity for starting new colonies. Inhibition of reproduction—a problem which social insects have solved long ago—expresses itself in complex tendencies that result in

increasing numbers of members of such a community leading non-reproductive lives, either from circumstantial, physiological or voluntary causes.

(5)—In communal life a regular, abundant and easily available source of food is one of the most urgent difficulties. Some of the smaller, and more primitive, insect societies are hunters that find their means of subsistence in a carnivorous diet. The more highly organized and densely populated colonies, on the other hand, rely as a rule upon the more abundant and easily procurable supplies afforded by the vegetable kingdom. The collecting and apportioning of food among adults and young, economy in its use, and competition with other organisms in obtaining supplies, find many parallels in human society. Thus, we find that social insects have established granaries and other storehouses: in the development of fungus beds they perform the rôle of cultivators, while the warrior caste has its place in insect society in all expeditions organized for the exploration of food resources further afield. The security and shelter afforded by the nests of social insects, as with human habitations and buildings, have been exploited by numerous alien inhabitants that are more or less tolerated by their insectan and human hosts. Means of communication are an essential attribute if social life is to endure and, consequently, we find among insects they similarly prevail. Tapping movements of parts of the body, particular deployment of the antennæ, stridulation, and the prevalence of specific odours, are all utilized for this purpose, although their detection and interpretation present many difficulties to us. Some measure of the biological success, of insect societies, must be ascribed to their adopting a mode of life which renders them little subject to the attacks of parasites and predators, which inflict such heavy mortality upon

most forms of insect life. Their chief enemies, as with human societies, are to be found in organized attacks by other communities. Termites, for example, have their sworn enemies in ants, and the more robust species of the latter creatures are the chief disturbers of the peace of the more weakly kinds.

(6)—Insect communities are immeasurably older than any human society. Even before our Simian ancestors had assumed any real semblance of human form, insect societies were as we find them to-day. As Wheeler has pointed out, a large part of the diet of these Simian ancestors probably consisted of those 'same ant species which had already developed a co-operative communism so complete that, in comparison, the most radical of our bolsheviks are ultra-conservative capitalists'. Ants, it may be added, can be traced as far back as Eocene times, while almost all their existing major groups occur in the Oligocene amber beds. During this latter epoch, we find that their castes were already sharply differentiated, and myrmecophiles had established their peculiar relationships. The development and establishment of insectan castes have taken place on an hereditary and instinctive basis, and they seem to have gained only in fixity during the vast interval of time that has since elapsed. Human society, already much behind in point of geological time, has evolved more speedily a non-hereditary caste system. The plasticity of its members is such that their inherited endowments, given adequate 'conditioning' by experience, can be so adapted that the normal individual is able to perform the usual functions of one or more castes. Insect society has developed solely upon a family basis and, although the family is the primitive basis of human society, the latter has now become national or even international in scope.

(7)—Among social insects we have seen that the com-

munity is virtually a vast proletariat of sterile working classes. Each individual member, uninfluenced either by rules or by legislation, labours with the utmost diligence ; its toils last the day long, and even night by no means always brings respite. Individual aspirations, comfort or pleasure find no place in such an economy, yet there is neither dissension nor strife. Individual lives are of little account, there are so many ; each is intimately merged into that of the community of which it is a part, and is unhesitatingly sacrificed in its service whenever occasion demands. We may pause and take comfort in the reflection that a social system of this kind is unattainable by any coercive or repressive manifestations on the part of the most ruthless human dictatorship.

APPENDIX ON LITERATURE

THE reader who desires to acquire something more than a mere epitome of the subject of social insects, as presented in this little volume, may turn to a number of books and scientific memoirs for additional information.

Their general biology, and the evolutionary phases in their behaviour, are dealt with in *Social Life among the Insects,** 1922, by W. M. Wheeler. A fuller and more recent treatment will be found in the same author's book, *The Social Insects,** 1928. The latter work, more especially, is a standard and is indispensable to all interested in the subject.

The various aspects of insect behaviour are discussed in several books, including *Forced Movements, Tropisms and Animal Conduct,* 1918, by J. Loeb ; *The Psychic Life of Insects,* 1922, by E. L. Bouvier (translation by L. O. Howard) ; *The Senses of Insects,* 1908, by A. Forel (translation by M. Yearsley), and *Ueber die ' Sprache ' der Bienen,* 1923, by K. von Frisch. The article ' Comparative Psychology ', by F. Hempelmann, in the latest edition of the *Encyclopædia Britannica,* should also be consulted.

The instinctive and plastic behaviour, of both solitary and social insects, has formed the subject of many works and is also dealt with in numerous others. The famous *Souvenirs Entomologiques* of J. H. Fabre are notable for the wealth and precision of the observations they contain : the significance of more plastic phases of behaviour, however, tends to be relegated to the background by Fabre, who remained uninfluenced by evolutionary theory. Other works include : *Wasps, Social and Solitary,* 1905, by G. W. and E. G. Peckham ; *Wasp Studies Afield,* 1918, by P. and

N. Rau; *La Vie des Abielles et des Guêpes,* 1923, by C. Ferton; *Die Europäischen Bienen,* 1923, by H. Friese; and *Ants, their Structure, Development and Behaviour,** 1910, by W. M. Wheeler, which is almost encyclopædic in the breadth of field covered. H. St. J. K. Donisthorpe's *British Ants,* 1927, may also be mentioned.

The only general account of termites is *Les Termites,** 1922, by E. Hegh, which contains a large amount of detailed information.

In so far as matters of wider entomological interest are concerned, a good introduction to insect structure and physiology, as exemplified by an individual species, is *The Anatomy and Physiology of the Honeybee,** 1925, by R. E. Snodgrass, while for a detailed treatment of insects as a class see *A General Textbook of Entomology,** 2nd edition, 1930, by A. D. Imms.

In addition to the foregoing, a large number of original memoirs are available for those who desire a deeper acquaintance with particular aspects of these several subjects. A mere list of these publications is too lengthy for inclusion here. A nearly complete bibliography of writings of this character will be obtained by consulting the references given in those books already quoted which are marked by an asterisk.

INDEX

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